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A developmental analysis of size and shape in tomato fruits

HELEN B. HOUGHTALING

(WITH PLATE 14)

To understand the way in which genes produce their effects it is of the utmost importance to find the visible changes which take place as a genetically controlled character develops. It has been the chief object of workers in the past to show that characters are inherited and to determine the chromosome mechanism involved. This work has been limited to the study of mature characters and the developmental aspect of the problem has largely been ignored. The object of the present study was to determine how differences in shape and size arise during development in the fruits of various genetically distinct types of *Lycopersicum esculentum* and in *L. pimpinellifolium*.

The work of Hedrick and Booth (1907), Price and Drinkard (1908), Groth (1915), Warren (1924), Lindstrom (1926-1932) and MacArthur (1925-1931) indicates a genetical basis for the inheritance of size and of shape in tomato fruits. Elongate shape is shown to be a single Mendelian recessive to spherical shape and has been located definitely in chromosome I. Size factors, although they have not been shown to give simple Mendelian ratios, have been found to be linked with specific characters such as fruit shape, color of epidermis, stem color and color of pericarp. Therefore, we may assume that the shapes and sizes which are to be studied in this paper are the results of gene activity.

MATERIALS AND METHODS

Seven varieties of *Lycopersicum esculentum* (table 1) differing as widely as possible in fruit size and shape, and the currant tomato, *L. pimpinellifolium*, were grown in the greenhouse during the winter of 1932. A number of hybrids were secured between the various types.

The hybrids and inbred lines from the original varieties were grown in the field during the summer of 1933. Material from these plants was fixed in 70% alcohol containing 6% formalin. Flowers were collected and fixed on the day of flowering. Stages before flowering and also developing fruits were fixed separately. Full-sized green fruits were collected early in September. These were weighed and then cut along the polar diameter and outlined on paper for a record of their shape and size. The number of car-

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pels was counted and a comparable portion of the pericarp of each fruit fixed. Volume of fruit and ovary was calculated from the dimensions by squaring the width (equatorial diameter), and multiplying it by the length, (polar diameter). This is thought to give a better measure of size than weight, since the specific gravity of the fruit changes rapidly as it ripens and is different in large and small fruited types (Lindstrom, 1926). More-

TABLE I

	FRUIT SIZE, CC.	SHAPE INDEX	NUMBER OF CARPELS	PERICARPING CELL SIZE MATURITY $\times 10^{-7}$ CC.	OVARY SIZE FLOWERING $\times 10^{-4}$ CC.	OVARY SHAPE AT INDEX FLOWERING	CELL SIZE AT FLOWERING $\times 10^{-10}$ CC.
Red Cherry	10.4	1.06W	2.00	78.7	16.6	1.27L	68.6
Red Plum	29.2	1.28L	2.00	150.0	22.9	1.87L	74.0
Red Pear	24.4	1.66L	2.00	91.7	29.2	2.25L	68.8
Yellow Pear	31.0	1.64L	2.00	173.0	20.7	2.61L	62.0
Red Peach	74.1	1.18W	2.60	138.0	45.0	1.08L	71.8
Yellow Peach	75.4	1.22W	3.20	225.0	31.4	1.22L	73.7
Bonnie Best	275.0	1.48W	4.25	268.0	161.7	1.53W	75.4
Red Currant	1.54	1.01W	2.00	18.4	5.1	1.27L	82.0
Plum×Cherry	15.0	1.01W	2.00	109.0	20.7	1.58L	79.8
Cherry×Y. Peach	19.7	1.14W	2.50	71.3	35.2	1.23L	73.9
R. Peach×Cherry	22.9	1.17W	3.20	96.0	13.3	1.23L	81.5
Frogmore×Cherry	44.1	1.22W	2.54	285.0	22.5	1.19L	83.2
R. Pear×Y. Peach	43.6	1.01L	3.24	139.0	28.4	1.37L	84.9
R. Cherry×R. Pear	14.9	1.03L	2.22	115.0	19.7	1.59L	74.0
Cherry×Bonnie Best	38.9	1.19W	3.16	153.0	50.2	1.02L	82.0
Bonnie Best×Cherry	41.8	1.23W	3.07	207.0	39.4	1.24L	86.5
R. Pear×Bonnie Best	72.0	1.05L	3.42	202.0	42.1	1.37L	78.8
Bonnie Best×Y. Pear	75.9	1.09L	3.71	395.0	22.8	1.52L	68.3
R. Pear×R. Plum	60.7	1.11L	3.60	196.0	24.3	1.33L	73.5
R. Pear×R. Peach	46.3	1.00	3.30	197.0	20.8	1.49L	78.7
Red Plum×R. Currant	4.2	1.03W	2.00	67.8	6.7	1.38L	82.2
Red Cherry×R. Currant	2.6	1.09W	2.00	34.6	5.0	1.15L	75.6

over, it was impracticable to get weight on very early stages of development and a value for fruit size was wanted which might be directly compared with values for the very early stages.

The material was imbedded in paraffin and sectioned, early stages 10 microns thick, later stages 15 and 20 microns thick. The early stages were projected at a magnification of 45x and 125x and measured from these projections. Later stages approaching one centimeter in diameter were measured directly. The values for mature fruits were taken from the outlines which had been drawn of them.

Cell size was measured in the ovary wall (later the pericarp). Transverse and longitudinal microtome sections showed the cells to be essen-

tially spherical except for very early stages when they were somewhat elongated along the polar axis. In measuring cells longitudinal sections were used throughout. The cells were projected at magnifications of 125x and 200x except for stages at flowering and before flowering, when the cells are so densely filled with protoplasm that the use of the projector was impracticable. Measurements on these early stages were made by a micrometer eye piece. The cells which were projected were drawn, a single field being chosen from the middle region of the pericarp in developing fruits, and two adjoining fields in the mature ones. The longest diameter and the diameter at right angles to this were measured on the ten largest cells. These were averaged and volume was computed (by employing the formula for the volume of a sphere). The geometric mean of the ten cells was computed and taken as the cell size in the individual fruits.

Measurements from five flowers (or fruits) were determined and were averaged to obtain the values for ovary (and fruit) size and for cell size.

All averages in table 1 are geometric. This is believed to give a truer value of the mean than an arithmetic average since all measurements are on growing tissues. The geometric mean was calculated by averaging the logarithms of the various values studied and finding the antilog of the average logarithm. The correlation tables and all charts are plotted on logarithmic scales. Standard errors of correlation coefficients are given.

DEVELOPMENT OF FRUIT

Cooper (1927) describes the development of the tomato flower using the varieties Bonnie Best and Greater Baltimore. Flowers are formed in a racemose cyme and several developmental stages may be found in a cluster so that it is not difficult to trace stages. From a more or less flat meristem sepal primordia arise, then petals and stamens and ovary primordia with a spiral order of origin. The ovary primordia elongate; the upper portion forms the stigma and style and the base thickens, forming the ovary. A placenta is formed, with developing ovules. Shortly after flowering the style falls off and the petals and stamens wither. The calyx enlarges and remains attached to the base of the developing fruit. The ovary continues to grow and develops into the mature fruit. Shortly after fertilization the placental tissue grows up around the ovules and the cells become very large, ultimately rupturing as the fruit becomes ripe.

DEVELOPMENT OF SHAPE

Shape differences may arise developmentally in a number of ways. Sinnott and Kaiser (1933) found that the difference in shape of two types of pepper (*Capsicum annuum*) is the result of different relative rates of

growth of length and width in developmental stages after flowering. In squash (*Cucurbita Pepo*) however, they found that the mature shape is not the result of such a differential growth rate, since it is already established in the early ovary primordium, and growth in the various dimensions proceeds at approximately the same rate.

The shape of the varieties of tomatoes studied here varies from the elongate pear type with length 1.65 times width to the flattened Bonnie Best whose width is 1.48 times its length. The hybrids vary in their relationship to the parent types but the general tendency is toward a spherical form.

In studying development of shape Huxley's formula (1932) $y=bx^k$ was employed. For shape, length (y) was plotted against width (x) logarithmically. The slope of the resulting line (or the value of k) measures the relative rate of growth of length and width.

Between flowering and maturity ovary length grows slightly more slowly than width, ($k=0.9$), but the relative growth of dimensions in all types after flowering is approximately equal, as it is in squash throughout development, so that shape is essentially determined by flowering. The correlation between shape at flowering and shape at maturity is $+.9198 \pm .0013$. The shape differentiation of the ovary thus takes place between the stage of the earliest flat primordium and the ovary of the flower. The ovary primordium of the pear grows rapidly in length at first with only slight increase in width ($k=1.80$) so that the elongate shape is established very early in development. The sphere forms also grow most rapidly in length in the early stages ($k=1.30$), and in the flattened types length grows only slightly faster than width ($k=1.03$). This is in marked contrast with the development of shape in peppers where types remain essentially the same up to flowering and differentiation occurs afterwards. In tomatoes the genes for shape act at a very early period and apparently operate by determining the relative polarity of cell division, since there is no marked difference in cell shape or size at this critical stage.

RELATIONSHIP OF SIZE AND SHAPE

Sinnott (1935) found no necessary relationship between size and shape in the second generation of crosses between large and small fruited squash and has presented evidence that the two aspects of development are quite independent of each other. Lindstrom (1929) found a relationship in tomatoes but concluded that it is caused by linkage between certain size and shape genes rather than by the mechanism through which shape is determined. In tomatoes shape is chiefly differentiated early in development but during later growth there is a slight added divergence since width in-

creases a little faster than length. Therefore in a pure line or F_1 a slight positive correlation between size and increased flattening might be expected. There is no significant correlation, however ($+.1776 \pm .1411$), between size and shape index in the tomato types studied here. Another factor enters the problem in that highly fasciated (multicarpellate) types tend to be both flatter and also larger than bicarpellate types. If *L. pimpinellifolium* and its hybrids, all of which are bicarpellate, are excluded the correlation between size and shape is higher ($.3402 \pm .0973$). The relationship between size and number of carpels is $+.7655 \pm .0115$ and between shape and the

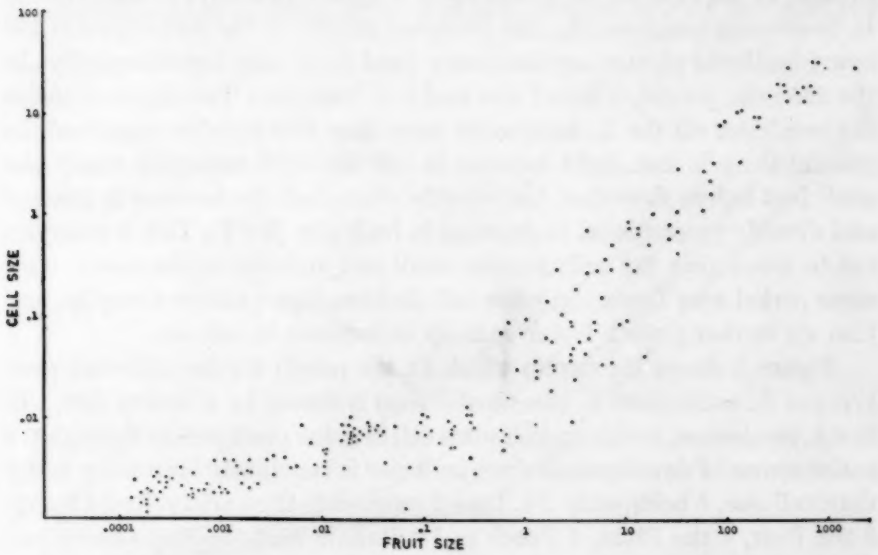

Fig. 1. Cell size plotted against fruit (and ovary) size, both logarithmically, throughout fruit development in all types of *Lycopersicum esculentum*. Fruit size in units of 10 cc.; cell size in units of 10^{-6} cc.

number of carpels is $+.4202 \pm .0701$. This latter relationship seems to be a mechanical one, for the fasciated types start from a broader meristematic platform than the others and the length of the ovary primordia would have to grow at a much greater rate with respect to width than has been observed in any of the fruit types to produce an elongate fasciated type within the period when shape is determined.

DEVELOPMENT OF SIZE

The size of the individual organ is associated with the original amount of growing tissue, the rate at which it grows and the point at which it stops growing. Sinnott (1921), Reed (1927) and Ashby (1932) conclude that ultimate size is determined largely by original size.

In the tomatoes here studied differences in fruit size are well established by the time of flowering (plate 14, figures 7 to 11) for the coefficient of correlation between ovary size at flowering and mature fruit size is $+.8789 \pm .0031$. Indeed, marked differences are evident at a much earlier stage, when the ovary primordium is just beginning its development, as is shown in figures 1 to 6. The size differences thus established early are maintained throughout development.

The problem arises as to whether these differences, which reach their culmination in the mature fruit, are associated with differences in number of cells, in size of cells, or in both these respects. In studying this problem in developing tomatoes the size (volume) of cells in the mid-region of the ovary wall was plotted against ovary (and fruit) size logarithmically. In the formula, $y = bx^k$, y is cell size and x is fruit size. Text figure 1 shows the result for all the *L. esculentum* pure lines and hybrids combined. In general there is but slight increase in cell size with enlarging ovary size until just before flowering, but shortly after that the increase is marked and directly proportional to increase in fruit size ($k = 1$). This is interpreted to mean that the cells remain small and actively meristematic until some period near flowering, when cell division ceases rather abruptly, and that all further growth is due entirely to increase in cell size.

Figure 2 shows the curves which fit the points for the different pure types of *L. esculentum*. *L. pimpinellifolium* is shown by a broken line. Unlike *L. esculentum*, in this species some cell division must persist through the entire course of development since fruit size is constantly increasing faster than cell size, k being only .74. Line 2 represents the variety Red Cherry, 3 the Pear, 4 the Plum, 5 Peach and 6 Bonnie Best. In Red Cherry cell division ceases relatively early in ovary development and cell enlargement stops when the cells are relatively small. In the Pear, cell division continues progressively further and cell size reaches a progressively higher value; and in the largest fruit, Bonnie Best, cell division persists the longest and cell size reaches its highest value.

The Cherry-Currant and Plum-Currant hybrids give curves intermediate between their parents. Cell division continues longer than in the esculentum types but not as long as in the pimpinellifolium. In general the curves of the esculentum crosses are intermediate between their parents. It is noteworthy that the shape of the developmental curve is essentially similar in all the varieties of *L. esculentum* though the abruptness of the change increases in the larger types. The length of the period during which cell division occurs (and thus the number of cells) and the degree of enlargement of these cells bear a rather constant relation to each other and both progressively increase as fruit size increases.

Fruit size at maturity is therefore related both to cell number and to cell size. Up to flowering the differences are all in cell number, for cell size is almost constant, the correlation between cell size and ovary size at flowering being only $+.0812 \pm .1760$. Final cell number is now established and is closely correlated with fruit size. However, the degree of cell enlargement is also related to mature fruit size, since cell expansion stops at progressively higher levels in the larger fruits with the result that there is a correlation of $+.9007 \pm .0020$ between cell size and fruit size at maturity. If cell number were the dominant factor in fruit size, the first part of the developmental curve would be as it is now, related to fruit size, and the

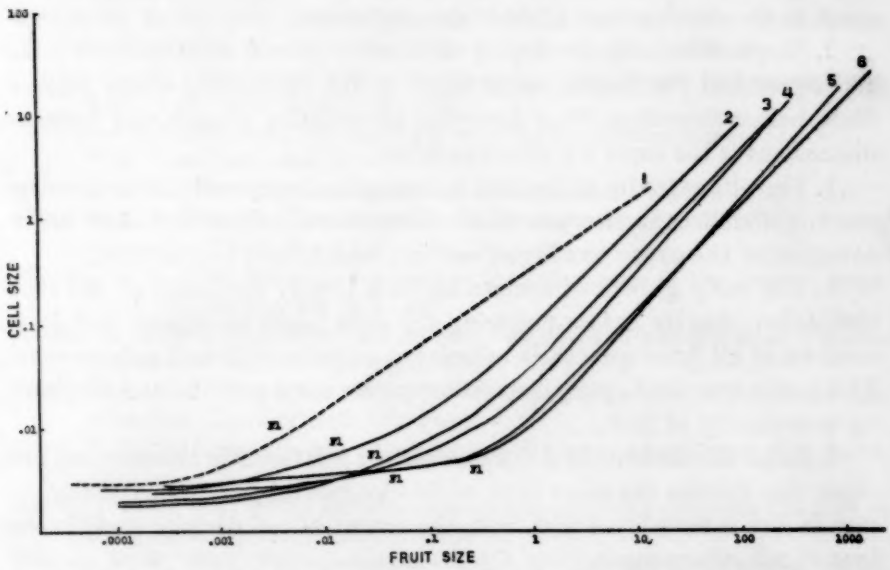

Fig. 2. Individual developmental curves for cell size plotted against fruit size, both logarithmically, in *L. pimpinellifolium* and in five types of *L. esculentum*. Line 1 (broken), *L. pimpinellifolium;* 2, Red Cherry; 3, Red Pear; 4, Red plum; 5, Red Peach; 6, Bonnie Best. *Fl*, size at flowering. Scale as in fig. 1.

second part would be of equal length in all types, reaching a uniform (and presumably optimum) cell size. If cell size were the dominant factor, the first part of the curve (cell number) would be uniform in all types and the second part would vary in extent. Neither of these conditions obtains, but the development of a particular size is the result of the combined action of both factors, cell size and cell number, acting in a specific and orderly fashion together. When this program has been completed growth stops. There is no obvious physiological reason why cell size in the Cherry type should not reach that attained by the Bonnie Best, but actually it stops

at about one third of this, at a point proportional to other points in development, such as the length of the meristematic period and the size at flowering.

We may conclude that size differences in the tomato fruits here studied are determined from the very beginning of development. The effect of these genetic differences is apparently upon an entire developmental program rather than upon any of its constituent factors.

SUMMARY

1. Seven pure breeding types of *Lycopersicum esculentum*, one type of *L. pimpinellifolium*, and fourteen F_1 progeny have been studied with respect to the development of fruit size and shape.

2. Shape differences develop by differential growth rates between polar and equatorial dimensions, established in the developing ovary primordium before flowering. After flowering the relative growth rate between dimensions is the same for all shape types.

3. The ultimate size of the fruit is determined very early in its development. Differences in size are visible in the floral primordia before differentiation of the ovary has begun and are maintained to maturity.

4. The early growth of tomato fruits is largely the result of cell multiplication; shortly before flowering the cells begin to enlarge and in *L. esculentum* all later growth is associated entirely with cell enlargement. This is not true for *L. pimpinellifolium* where some cell division continues up to maturity of fruit.

5. In all the varieties of *L. esculentum* the relationship between cell and organ size follows the same type of developmental program. Differentiation in size is associated with both the extent of cell division and the extent of cell enlargement.

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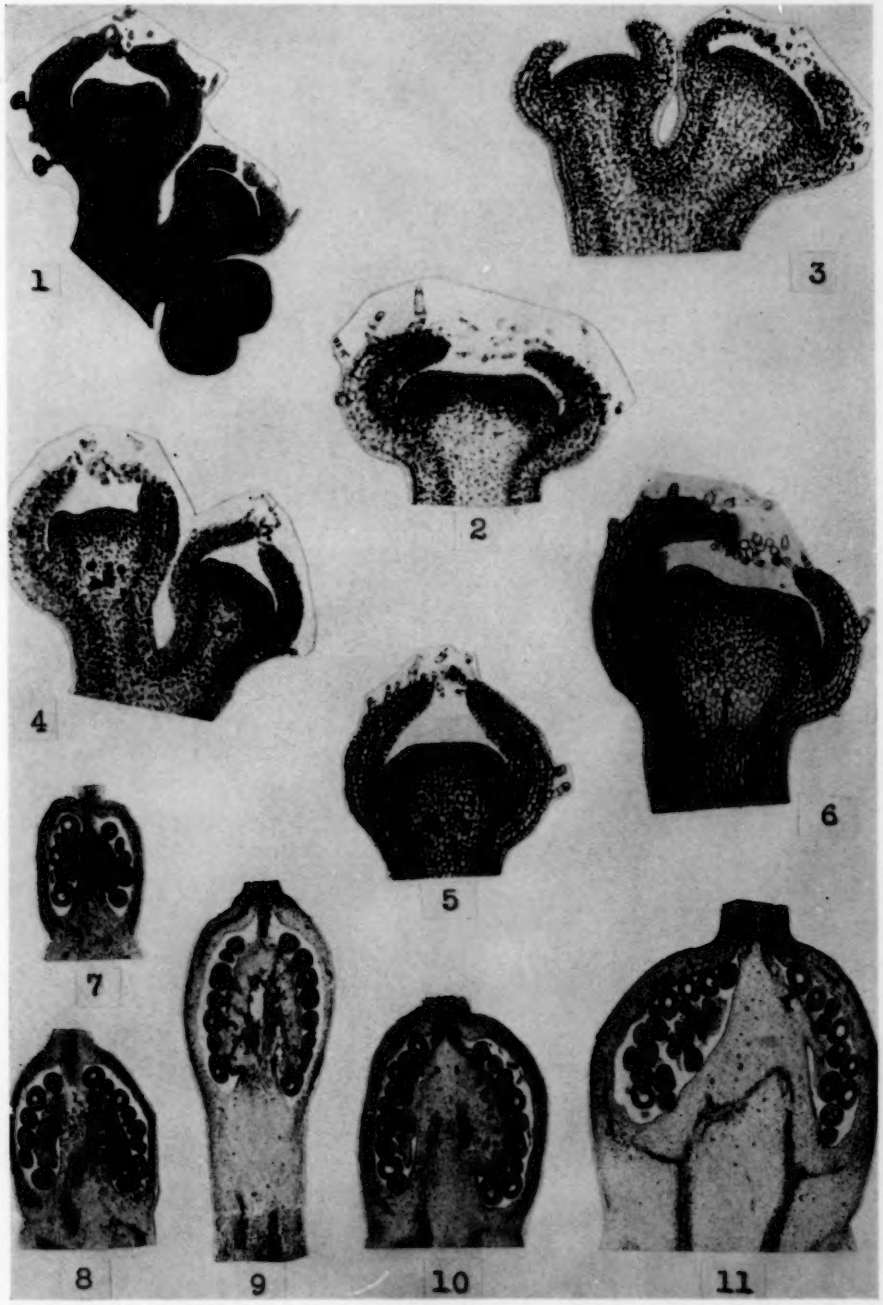
Explanation of plate 14

Figs. 1–6. Flower primordia, all ×90

1. Red Currant, *L. pimpinellifolium*
2. Bonnie Best×Red Cherry, *L. esculentum*
3. Red Peach
4. Red Cherry×Red Currant
5. Red Pear
6. Bonnie Best

Figs. 7–11. Ovaries at flowering, all ×20

7. Red Currant
8. Red Cherry
9. Red Pear
10. Red Peach
11. Bonnie Best



HOUGHTALING: TOMATO FRUITS

DUKE MICH

The genus Cheilophyllum of the West Indies

FRANCIS W. PENNELL

Some years ago, when studying the Cuban species of the family Scrophulariaceae, I realized that the little trailing plant which Grisebach had described as *Stemodia radicans* lacked the anther-structure peculiar to that genus; its closely contiguous cells showed that this species belonged with the more typical members of the tribe Gratioleae, although certain characters marked it as a distinct and rather remote genus. Accordingly in 1920 I established for it the new genus *Cheilophyllum*, so called from the Greek χειλος, margin, and φύλλον, leaf, in allusion to the thickened edges of the leaf-blades. Later, in my account of the "Scrophulariaceae of Cuba" (in Proc. Acad. Nat. Sci. Philadelphia **75**: 5. 1923), the position of the genus was shown in more detail by comparing it with others of this family in the Cuban flora.

The few collections seen did not suggest to me that *Cheilophyllum* could be other than monotypic, though occurring in both Cuba and Jamaica. But in 1931, in his study of Dr. E. L. Ekman's extensive collections, the late Dr. Ignatius Urban, after adopting my generic proposal, added four more species, all from Cuba. Despite my high regard for the opinion of the veteran student of the West Indian flora, I must confess that I was at first wholly skeptical about the validity of the new species. Thanks, however, to the receipt by the New York Botanical Garden of isotypes of three of the four species, supplied from the Natural History Museum at Stockholm, Sweden, I now gladly endorse all of Urban's proposed species, and must add yet three others, thus bringing the number in this genus to eight.

These little plants, which are so rarely collected, show considerable and seemingly constant differences between what appear to be well marked species. Most of these are known, however, from single or few collections, and the group should be revised again after the assembling of much more ample material. The following tentative outline is to show the present state of knowledge about this endemic Antillean genus.

Specimens have been reviewed in the following herbaria, each designated in the text by a symbol:

H—Gray Herbarium, Harvard University, Cambridge, Massachusetts;
Ph—Academy of Natural Sciences, Philadelphia, Pennsylvania;
Y—New York Botanical Garden, New York City.

CHEILOPHYLLUM Pennell

Cheilophyllum Pennell; Britton in Mem. Torrey Bot. Club **16**: 103. 1920. Genotype, *Stemodia radicans* Griseb.

Corolla 5.5 mm. long; style 2.5 mm. long; leaf-blades elliptic or lanceolate, the thickened margin usually two-toothed. 1. *C. macranthum*

Corolla 1.5–3 mm. long; style 0.5–1 mm. long.

Capsule ovoid, 2–2.5 mm. long, equaled or scarcely exceeded by the sepals; style 1 mm. long; leaf-blades elliptic to nearly circular, dentate.

Leaf-blades oval or wider, with thickened recurved margins; sepals acute.

Apex of the slightly margined leaf-blades obtuse or rounded; internodes less than twice the length of the leaves; plant somewhat pubescent.

Leaf-blades widely oval or nearly circular, broadly rounded, pubescent and obscurely punctate beneath, 3–5 mm. long; stem, pedicels, and sepals pubescent, the hairs obscurely or not glandular; stems long, little branched, 10–20 cm. long. 2. *C. radicans*

Leaf-blades oval, obtuse or somewhat rounded, glabrous and prominently punctate beneath, 2–4 mm. long; stem glabrous; pedicels, and especially sepals, sparsely glandular-pilose; stems shorter, much branched, only 3 to 5 cm. between plantlets. 3. *C. microphyllum*

Apex of leaf-blades acute; internodes 2 to 4 times the length of the leaves.

Stem and leaves glabrous, the latter strongly margined; pedicels 4–6 mm. long; internodes 3 to 4 times the length of the leaves. 4. *C. marginatum*

Stem glandular-pubescent; leaves with midrib somewhat pubescent beneath, the blades only slightly margined; pedicels 2–3 mm. long; internodes usually the length of the leaves. 5. *C. jamaicense*

Leaf-blades elliptic, the margin slightly, if at all, thickened or recurved; sepals attenuate, glandular-pilose. 6. *C. dentatum*

Capsule short-ovoid or globose, 1–1.5 mm. long, exceeded by the sepals; style 0.5–0.7 mm. long; leaf-blades elliptic or elliptic-lanceolate, entire or nearly so.

Pedicels 3–4 mm. long, shorter than or equaling the bracts; leaf-blades 4–5 mm. long; sepals and pedicels glandular-pubescent. 7. *C. micranthum*

Pedicels 5–8 mm. long, exceeding the bracts; leaf-blades 3–4 mm. long; sepals and pedicels sparsely glandular-pilose or glabrate. 8. *C. sphaerocarpum*

1. CHEILOPHYLLUM MACRANTHUM Urban.

Cheilophyllum macranthum Urb. in Arkiv Bot. **23A**. n.11: 39. 1931. "Cuba, prov. Santa Clara prope Mordazo ad Laguna Yaiti, . . . [E. L. Ekman] n. 17104." Type not seen nor verified, but apparently well distinguished by its large flower; the fruit is still unknown.

Middle Cuba.

CUBA. Santa Clara: Mordazo, Ekman 17104.

2. CHEILOPHYLLUM RADICANS (Grisebach) Pennell.

Stemodia radicans Griseb., Cat. Pl. Cub. 182. 1866. "Cuba occ. (Wr[ight] 3006), in savannis pr[ope] Hanabana (Wr[ight] a-1865)." Isotypes of Wright 3006 have

been seen in Gray Herbarium and New York Botanical Garden; at the former accompanied by penciled descriptive and locality notes, the latter being "sandy pinales. Dec. 2. Asiento viejo to Remates." At both institutions Wright 3006 contains two species intermixed, the present and the following, but the sheet that bears this geographic information bears only the present species. These localities are in Pinar del Rio, and nearly at the western extremity of Cuba. While the description was based upon both components, it was clearly the long, repeatedly rooting stems of the present plant that suggested the specific name. The plant from Hanabana appears to be lacking in American herbaria.

Sandy pineland, western Cuba.

CUBA. Pinar del Rio: Asiento viejo to Remates, C. Wright 3006 p.p. (H,Y).

3. **Cheilophyllum microphyllum** Pennell, sp. nov.

Stems strongly ridge-angled, glabrous, much branched, only 3 to 5 cm. long between plantlets. Leaf-blades 3–4 mm. long, oval, acutish to somewhat rounded, slightly crenately dentate, glabrous, glandular-punctate, narrowed to sessile or shortly petiolar bases, the margin slightly incurved and callose-thickened. Pedicels 2–4 mm. long, slightly glandular-pilose. Sepals 1.5–2 mm. long, lanceolate, attenuate, finely glandular-pubescent. Corolla 3 mm. long, white, the tube slightly pubescent within, the lobes slightly longer than the tube, the posterior wider, nearly distinct or much united. Anthers 0.3 mm. long. Style 1 mm. long. Capsule 2–2.5 mm. long, ovoid, acute. Seeds not seen.

(Caulis ramosissimus, glaber; folia 3–4 mm. longa, ovalia, obtusa, dentata, glabra, punctata, margine paulum incrassata; pedunculi 2–4 mm. longi; sepala 1.5–2 mm. longa, minute glandulo-pilosa; corolla 3 mm. longa; capsula 2–2.5 mm. longa, ovoidea, acuta.)

Type, western Cuba ("Cuba occ."), collected in flower and fruit by Charles Wright, no. 3006 p.p., in Gray Herbarium of Harvard University; isotypes in Herb. New York Botanical Garden and Academy of Natural Sciences of Philadelphia.

Western Cuba.

CUBA. Pinar del Rio, Wright 3006 p.p. (H,Ph,Y).

4. **Cheilophyllum marginatum** Pennell, sp. nov.

Stems strongly ridge-angled, glabrous, little branched above base, reaching 10 to 15 cm. long. Leaf-blades 3–5 mm. long, oval, acute, distally with one or two pairs of more or less sharp teeth, relatively glabrous, strongly glandular-punctate, narrowed to shortly petiolar bases, the margin strongly incurved and callose-thickened. Pedicels 4–6 mm. long, very sparsely glandular-pilose. Sepals 2–2.5 mm. long, linear-lanceolate, glabrous. Corolla 2.5 mm. long, white, the tube slightly pubescent within, the lobes slightly longer than the tube, the posterior little if at all wider, and apparently only partially united beyond the others. Anthers 0.3 mm. long. Style about 1 mm. long. Capsule 2.5 mm. long, ovoid, acute. Seeds 0.3 mm. long, 0.2 mm. wide, brownish-black, minutely ridged.

(Caulis paulum ramosus, glaber; folia 3–5 mm. longa, ovalia, acuta, dentata, glabrata, punctata, margine forte incrassata; pedunculi 4–6 mm. longi; sepala 2–2.5 mm. longa, glabra; corolla 2.5 mm. longa; capsula 2.5 mm. longa, ovoidea, acuta.)

Type, Placetas del Sur, Santa Clara, Cuba, collected in flower and fruit August 10, 1918 by Bro. Leon and Ter. M. Roca, no. 8150; in Herb. New York Botanical Garden.

Middle Cuba.

CUBA. Santa Clara: Placetas del Sur, Leon & Roca 8150 (Y); Sagua, N. L. Britton & P. Wilson 330 (Y).

5. **Cheilophyllum jamaicense** Pennell, sp. nov.

Stems ridge-angled, minutely glandular-pubescent, much branched at base, the branches reaching 15 to 25 cm. long. Leaf-blades 4–7 mm. long, oval, acute, with one or two pairs of rounded or rather sharp teeth, glabrous except on the midrib beneath, glandular-punctate, cuneately narrowed to sessile or scarcely petiolar bases, the margin incurved and slightly callose-thickened. Pedicels 2–3 mm. long, glandular-pubescent. Sepals 2.5 mm. long, lanceolate, glandular-pubescent. Corolla white, seen only in bud. Style 0.7 mm. long. Capsule 2 mm. long, ovoid, acute. Seeds not seen.

(Caulis pubescens, ramosissimus; folia 4–7 mm. longa, ovalia, acuta, dentata, glabrata, punctata, margine incrassata; pedunculi 2–3 mm. longi; sepali 2.5 mm. longa, pubescentia; capsula 2 mm. longa, ovoidea, acuta.)

Type, growing in shade of grasses, Ashley Hall Savanna, Lower Clarendon, Jamaica, alt. 100 ft. (30 m.), collected in flower and fruit December 6, 1917, by William Harris, no. 12737; in Herb. New York Botanical Garden.

Grassland, Jamaica.

JAMAICA. Lower Clarendon: Ashley Hall Savanna, Harris 12737 (H,Ph,Y).

6. CHEILOPHYLLUM DENTATUM Urban.

Cheilophyllum dentatum Urb. in Arkiv Bot. **23A**. n. 11: 41. 1931. "Cuba, prov. Santa Clara prope Motembo in savannis humidis, . . . [Ekman] n. 16810." Isotype, collected June 27, 1923, seen in Herb. New York Botanical Garden.

Grassland, middle Cuba.

CUBA. Santa Clara: Motembo, Ekman 16810 (Y).

7. CHEILOPHYLLUM MICRANTHUM Urban.

Cheilophyllum micranthum Urb. in Arkiv Bot. **23A**. n. 11: 40. 1931. Cuba, prov. Camaguey ad kilom. 9 lineae ad Nuevitas versus in Carrascales (v. Cuabales). . . . [Ekman] n. 15567." Isotype, collected October 21, 1922, seen in Herb. New York Botanical Garden.

Middle Cuba, Carrascales.

CUBA. Camaguey: at km. 9 of the line to Nuevitas, Ekman 15567 (Y).

8. CHEILOPHYLLUM SPHAEROPHYLLUM Urban.

Cheilophyllum sphaerocarpum Urb. in Arkiv Bot. **23A**. n. 11: 39. 1931. "Cuba, prov. Santa Clara prope Motembo in palmetis, . . . [Ekman] n. 16826." Isotype, collected June 27, 1923, seen in Herb. New York Botanical Garden.

Gravelly soil, along streams and in palm groves middle Cuba.

CUBA. Santa Clara: Motembo, Ekman 16826 (Y); Sabana de Motembo, Bro. Leon & A. Loustalat 9361 (Y), 11341 (Ph,Y).

ACADEMY OF NATURAL SCIENCES OF PHILADELPHIA

The anatomy of the stem in the Lejeuneae

ALEXANDER W. EVANS

(concluded)

Paradoxae

COLURA ORNATA Goebel. In the genera *Colura* and *Diplasiolejeunea* the underleaves are duplicate; that is, there is one underleaf for every lateral leaf, instead of one for every two lateral leaves, as in the Holostipae and Schizostipae. In spite of this peculiar feature both genera show the simplified type of stem-structure found in the last four of the Schizostipae under consideration. In other words the cortical cells are in seven longitudinal rows and the medullary cells in three. The genus *Colura* is largely tropical and includes many epiphyllous species, of which the East Indian *C. ornata* is a characteristic example. The irregularly branched stems of this pale green plant are mostly 1–2 cm. in length, about 0.1 mm. in width, and about 0.06 mm. in thickness. Cross-sections, in consequence, are elliptical (fig. 7, A). The cortical cells measure 25–40μ width by 15–30μ in thickness, and those of the two ventral rows are distinctly smaller than the others. The medullary cells average about 25μ in diameter. The unpigmented cell-walls are thin or slightly thickened, and the bounding walls may be as much as 4μ thick. In the interior indistinct triangular thickenings can be demonstrated where three cells come together.

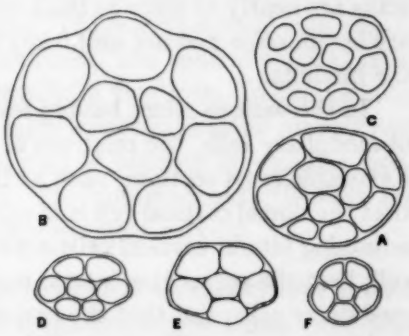


Fig. 7. Cross-sections of stems. A *Colura ornata* Goebel. B. *Diplasiolejeunea unidentata* (Lehm. & Lindenb.) Schiffn. C. *D. pellucida* (Meissn.) Schiffn. D. *Leptocolea planifolia* Evans. E. *L. scabriflora* (Gottsche) Evans. F. *Aphanolejeunea microscopica* (Tayl.) Evans. All, ×225.

DIPLASIOLEJEUNEA UNIDENTATA (Lehm. & Lindenb.) Schiffn. Except for a few extra-tropical species the genus *Diplasiolejeunea* is tropical and includes both corticolous and epiphyllous representatives. The West Indian *D. unidentata* may be chosen as an example of the first group The pale green plants of this rather robust species form irregular or radiating patches, and the sparingly pinnate stems, which are about 0.14 mm. in diameter, may attain a length of 2.5 cm. The cell-walls, as seen in cross-section, show a pale brownish yellow pigmentation. The cortical cells (fig. 7, B) measure 40–50μ in width and thickness, and the medullary cells average

about 35μ in diameter. The outer walls of the stem are 6–8μ thick, but the other walls are mostly only 3–4μ thick, except for the more or less distinct triangular thickenings, wherever three cells come together.

DIPLASIOLEJEUNEA PELLUCIDA (Meissn.) Schiffn. The present species, which is representative of the epiphyllous forms of the genus, has a wide distribution in tropical America and is known also from Africa. Although the irregularly branched, pale green plants may be as much as 2 cm. in length, they are more delicate than in *D. unidentata*, and the stems average only 0.085 mm. in width by 0.06 mm. in thickness. The cortical cells (fig. 7, C) are 25–30μ in width by 15–20μ in thickness, and their walls are 4–6μ thick. The medullary cells average about 20μ in diameter, and their walls are nearly or quite as thick as those of the cortical cells. All the walls are cream color and are uniformly thickened, except for occasional pits in the medulla.

In the various stems having seven rows of cortical cells and three rows of medullary cells, the relations of symmetry are of considerable interest. Favorable cross-sections, such as the one represented in figure 7, B, show that the dorsal cortical cell is in contact with two medullary cells, that the adjoining lateral cortical cells are each in contact with a single medullary cell, that the succeeding lateral cortical cells are each in contact with two medullary cells, and that the two ventral cortical cells are each in contact with a single medullary cell. If these relationships are kept in mind it will be seen that the only axis of symmetry is a vertical line passing through the middle of the dorsal cortical cell, between the two lateral medullary cells, through the middle of the ventral medullary cell, and between the two ventral cortical cells. These highly simplified stems, therefore, exhibit bilateral symmetry only and thus differ from the more generalized type of stem found in *Taxilejeunea pterogonia*, in which a radial symmetry has been demonstrated.

LEPTOCOLEA PLANIFOLIA Evans. The genus *Cololejeunea*, as originally defined, included all the Lejeuneae without underleaves. In place of these structures the ventral segments of the stem develop radicelliferous cells or groups of cells, which have the power of growing out into rhizoids. As pointed out by Goebel (1928, p. 25) the radicelliferous cells or groups of cells are duplicate, just as the underleaves are duplicate in *Colura* and *Diplasiolejeunea*. The absence of underleaves, which in itself indicates an advanced stage of development from the standpoint of evolution, is associated with the most highly simplified, or advanced, type of stem-structure to be found in the Lejeuneae. The stems, in other words, have only five or six rows of cortical cells and only a single row of medullary cells. The rows

of cortical cells include two on each side in a lateral (or dorsi-lateral) position and one or two in a ventral position. In certain cases the number of ventral rows may be increased to three in the vicinity of the radicelliferous cells, but the normal number for a given species is one or two.

During recent years several groups of species have been separated from *Cololejeunea* as distinct genera, and *Leptocolea* represents one of these segregates. It is composed of corticolous and epiphyllous species, most of which are tropical, and includes some of the more robust Lejeuneae without underleaves. In spite of this fact the species of *Leptocolea* are delicate and fragile. The pale green plants of *L. planifolia*, a Porto Rican species, form depressed mats on living leaves. The individual stems are irregularly branched and measure, in most cases, 0.5–1 cm. in length, about 0.06 mm. in width, and about 0.045 mm. in thickness. The lateral cortical cells (fig. 7, D) are 20–25μ in width by 12–20μ in thickness. The ventral cortical cells, which may be a little smaller, are normally in two rows. In the vicinity of the radicelliferous cells, however, an additional row may be present and on slender branches the number of rows may be reduced to one. The medullary cells are about 20μ in diameter. The unpigmented cell-walls are thin or slightly thickened, but the thickness rarely exceeds 2μ.

LEPTOCOLEA SCABRIFLORA (Gottsche) Evans. This epiphyllous species is widely distributed in tropical America, particularly in Brazil. The pale green, sparingly branched stems, which grow scattered or in depressed mats, are about 1 cm. long, 0.05 mm. in width, and 0.04 mm. in thickness. The cortical cells, which are in five rows (fig. 7, E), are mostly 14–20μ in width by 10–14μ in thickness, and the medullary cells average about 14μ in diameter. The bounding walls of the lateral cortical cells are 2–3μ thick, but all the other walls are thin, except for minute triangular thickenings at the angles.

APHANOLEJEUNEA MICROSCOPICA (Tayl.) Evans. The genus *Aphanolejeunea* is another segregate from the genus *Cololejeunea* as originally defined. The species are minute and delicate and grow for the most part on bark and living leaves. Although the genus is largely tropical the type-species, *A. microscopica*, is known only from a few scattered localities in western Europe, where it grows on rocks and trees, usually in company with other hepatics. The fragile pale green stems, which branch sparingly, rarely exceed 0.5 cm. in length and average about 0.04 mm. in diamteer. The cortical cells, four rows of which are lateral and one ventral (fig. 7, F), bulge slightly and measure about 20μ in width by 15μ in thickness. The medullary cells average about 10μ in diameter, and the colorless cell-walls are all about 2μ thick.

In such species as *Leptocolea scabriflora*, in which a certain amount of dorsiventral flattening is apparent in the stem, the vertical median plane is the only plane of symmetry present, and the stem is therefore a bilateral organ, comparable in this respect with the stems of *Microlejeunea bullata*, *Diplasiolejeunea unidentata*, and other species having seven rows of cortical cells and three rows of medullary cells. In such species as *Aphanolejeunea microscopica*, however, in which there is no dorsiventral flattening of the stem, each plane passing through a row of cortical cells and between the opposite pair of rows is a plane of symmetry. There are therefore four oblique planes of symmetry in addition to the vertical plane, making five in all. The stem in consequence is a radial organ, comparable with the stems of *Taxilejeunea pterogonia* and similar forms with seven planes of symmetry.

In the writer's experience the stems of *Leptocolea scabriflora* and *Aphanolejeunea microscopica* are representative of the most simplified types of stem-structure found in the Lejeuneae. Goebel, however, has described a still more simplified type in a Sumatran species of *Aphanolejeunea*, to which he has given the name *Physocolea* (*Aphanolejeunea*) *proboscoidea* (1928, p. 38). In the normal stem of this species, according to his account, there are only three rows of cortical cells surrounding the axial row of medullary cells; and it is further stated that the medullary row may be absent and that the stem, under these circumstances, consists of three longitudinal rows of cells meeting in the axis.

It is unfortunate that Goebel did not figure cross-sections of these simplified stems. The figure which he cites as illustrating the normal type of structure (1928, *pl. 6, f. 63*) need not necessarily be interpreted in the way he suggests. The figure in question represents the ventral surface of a stem, and the three rows of cells shown are the ventral row of cortical cells (with the radicelliferous cells clearly indicated) and a lateral row of cortical cells on each side. A stem with five rows of cortical cells would present the same appearance, since the two lateral rows meeting in the middle of the dorsal surface would be concealed by the two rows shown. His other figures of stems, which represent a closely allied species (1928, *pl. 6, f. 68, 70, 71*), might equally well have been drawn from stems with five rows of cortical cells. It may be recalled that Leitgeb described and figured very young stems of *Trichocolea tomentella* (Ehrh.) Dumort. and *Chiloscyphus pallescens* (Ehrh.) Dumort., in which cross-sections showed only three cells meeting in the center (1875, p. 6, footnote; *pl. 3, f. 18c; pl. 6, f. 16b*). These stems, however, were so young that rudimentary leaves had not yet made their appearance, and with the appearance of leaves the arrangement of the cells in the stem at once became more complicated. This was brought

about by the cutting off of medullary cells and by an increase in the number of the outside cells, now representing the cortex. It would hardly be expected that the stem of one of the Lejeuneae, with its highly specialized, complicate-bilobed leaves, could be simplified to such an extent that these leaves would arise from a single row of cells, although cases are known where they arise from two rows, one of which gives off the lobe and the other the lobule. It is of course possible that Goebel's observations may have been made on stems which were still in a juvenile stage of development, but in any case the confirmation of his statements is much to be desired.

GENERAL DISCUSSION

Various features of the Lejeuneae indicate that the group is relatively "advanced" from the standpoint of evolution. In a group of this character, which contains many diverse elements, it is exceedingly difficult to interpret the details of stem anatomy in terms of phylogenetic relationship, although certain evolutionary trends can be distinguished more or less clearly. It is perhaps safe to assume, in a broad way, that the more generalized types preceded the more specialized types, and that the latter arose through processes of differentiation or reduction or perhaps through combinations of the two. Few students, for example, would maintain that the highly simplified stems found in the Paradoxae and in many of the Schizostipae represent primitive conditions. They represent, rather, advanced conditions in which the process of reduction has proceeded toward an extreme limit.

The more generalized types of stems in the Hepaticae are those in which the differentiation into tissues is slight and in which the component cells are numerous and irregular in their arrangement. If these criteria are applied to the Lejeuneae it will be seen that the stems of certain Holostipae conform more or less closely to the generalized condition. In *Neurolejeunea Breutelii*, for example, cross-sections of stems (fig. 3, C) bring out very slight differences between the cortical and medullary cells, and the same thing is true of *Omphalanthus filiformis* (fig. 3, H). Both cortex and medulla, moreover, are composed of an indefinite but fairly large number of cells, and the arrangement of these cells tends to be irregular. Macerated preparations (fig. 3, D–G, I–N), to be sure, show that the differences between the cortical and medullary cells are greater than the cross-sections indicate; but, even so, these stems approach the theoretically generalized condition more closely than those of most Lejeuneae.

Passing from the more generalized types of stem-structure, two divergent lines of evolutionary advance can apparently be recognized, one leading to more complex and more highly differentiated conditions and the

other to more simplified conditions. The stems of such species as *Bryopteris filicina* (fig. 1) and *Ptychanthus striatus* (fig. 2) exemplify the first line of advance. In these stems the number of component cells, in comparison with the *Neurolejeunea* and the *Omphalanthus*, is greater, the differences between the cortical and medullary cells are more pronounced, and the medulla itself is differentiated into various kinds of cells. These stems, it will be remembered, maintain in the air a more or less horizontal position and are thus exposed to unusual conditions. Their increased size and more marked differentiation must help them in withstanding the environmental dangers to which they are subjected, and the teleologist might explain their complex structure on the basis of adaptation. However this may be, the stems in question apparently represent an advance from a more generalized condition, although the possibility of a progress in the opposite direction can not be altogether ignored.

In the evolutionary advance toward simplification, an increase in the size of the cortical cells, accompanied in most cases by a decrease in their number, may be looked upon as an initial step. The stems of *Brachiolejeunea insularis* (fig. 5, A), *Dicranolejeunea axillaris* (fig. 5, B), and *Odontolejeunea lunulata* (fig. 5, D) illustrate this condition clearly. The cortical cells in these stems are distinctly larger than the medullary cells and, in the *Dicranolejeunea* and the *Odontolejeunea* at least, are arranged in only ten longitudinal rows. In *Anoplolejeunea conferta* (fig. 5, E) the process of reduction has gone a little farther, and only seven rows of cortical cells are present. It has already been pointed out that seven rows of cortical cells are to be found in the vast majority of the Schizostipae, as well as in the Paradoxae with underleaves.

The stems of the Schizostipae, if the group is taken as a whole, are more simplified or advanced than those of the Holostipae. Not only is this the case but the process of reduction can be clearly followed within the group. In doing this the very few species with more than seven cortical cells, such as *Potamolejeunea orinocensis* (fig. 6, A), may be left out of consideration, and such a species as *Taxilejeunea pterogonia* (fig. 6, B), with seven rows of cortical cells and a large, well-differentiated medulla, may be chosen as having a relatively primitive type of stem-structure. Starting with such a stem it will be found that the reduction has not involved the number of cortical cells but has involved, in a marked degree, the number of medullary cells. In *Taxilejeunea pterogonia*, for example, about thirty-five medullary cells appear in cross-sections of the stems; in *Cystolejeunea lineata* (fig. 6, I), however, only about twenty-five are present, in *Hygrolejeunea cerina* (fig. 6, H) about twenty, in *Lejeunea flava* (fig. 6, L) about thirteen, and in *Pycnolejeunea macroloba* (fig. 6, K) about eleven. The proc-

ess of reduction within the group reaches its ultimate stage in such species as *Drepanolejeunea inchoata* (fig. 6, O), *Leptolejeunea elliptica* (fig. 6, P), and *Microlejeunea bullata* (fig. 6, N), in which cross-sections show only three medullary cells.

The type of stem-structure illustrating the ultimate stage of reduction in the Schizostipae corresponds with the primitive type of structure in the Paradoxae. This is found in forms with underleaves, and is exemplified by such species as *Colura ornata* (fig. 7, A), *Diplasiolejeunea unidentata* (fig. 7, B), and *D. pellucida* (fig. 7, C). As already pointed out, however, the reduction has proceeded still farther in forms without underleaves and has involved both cortical and medullary cells. In *Leptocolea scabriflora* (fig. 7, E) and *Aphanolejeunea microscopica* (fig. 7, F), for example, cross-sections of stems show only five cortical cells surrounding a single medullary cell.

It may be noted that the cell-differentiation, which is so pronounced in some of the more complex stems of the Holostipae and Schizostipae, tends to become less so as the process of reduction goes on. This may be illustrated by such a series as *Taxilejeunea pterogonia*, *Hygrolejeunea cerina*, *Lejeunea flava*, *Leptolejeunea elliptica*, and *Aphanolejeunea microscopica*. In the last two members of this series the histological differences between the cortical and medullary cells are very slight.

The stems of the Lejeuneae perform various physiological functions and exhibit, in varying degrees, a division of labor. The process of absorption, for example, even in the most simplified stems, is carried on by the cortical cells; and it has already been pointed out that these cells, in stems with a large-celled cortex (see, for example, page 202), may represent also an important photosynthetic tissue, with the storage of water as a possible subsidiary function.

In the smaller and more simplified stems the most important functions are undoubtedly absorption and photosynthesis. In larger and more complex stems, however, the maintenance of rigidity and the transportation of aqueous solutions become increasingly important. This is particularly true of such species as *Bryopteris filicina* (fig. 1), *Ptychanthus striatus* (fig. 2), and *Stictolejeunea Kunzeana* (fig. 3, A), in which relatively large branch-systems, spreading out horizontally in the air, are produced. In the stems of these species the peripheral medullary cells are characterized by their fiber-like form, very thick walls and small lumina. Cells of this character, by their structure and position, are clearly of use in resisting bending forces. They are associated with similar thick-walled cells having thin oblique or transverse walls at the ends. Such cells supplement the fiber-like cells as skeletal elements and, at the same time, afford facilities for the transportation of solutions in a longitudinal direction.

Although the thick-walled cells in the species just discussed are significant as supporting structures, there are other species with thick-walled cells in which the stems are scarcely or not at all exposed to bending or crushing forces. The species in question have prostrate stems, closely adherent to the substratum or growing in depressed mats. As examples *Omphalanthus filiformis* (fig. 3, H), *Leucolejeunea xanthocarpa* (fig. 3, O), and *Pycnolejeunea macroloba* (fig. 5, K) might be cited. What is the significance of the thick cell-walls in such cases? In the opinion of Goebel (1915, p. 553) thick cell-walls in the bryophytes owe their chief value to their power of absorbing water rapidly by imbibition. He therefore looks upon them as a xeromorphic feature, whereby the plants possessing them are enabled to resume their physiological activities quickly and effectively after periods of dryness. In opposition to this view it might perhaps be urged that many of the Lejeuneae and other bryophytes with thick cell-walls grow in habitats which are well supplied with water, rather than in dry habitats. Even in favorable localities, however, periods of abundant water-supply may be interrupted by periods of dryness, during which plants growing in exposed situations may be subjected to xerophytic conditions. Since these plants are unprovided with cuticular coverings of any sort they tend to lose much of their water and to pass quickly into a condition of inactivity. This is the case with the Lejeuneae under consideration. Their thick cell-walls, therefore, might well have the significance which Goebel would assign to them.

THE RELATIONSHIP BETWEEN THE SEGMENTS AND THE ADULT STEM

In the development of the shoot the Holostipae and Schizostipae conform to the type which is found in the vast majority of the acrogynous Jungermanniales. In this type the development is by means of an apical cell with three cutting faces, two of which are lateral and the third ventral. The segments cut off from the apical cell are parallel with these faces and arise in a spiral sequence (fig. 8, E). In other words a ventral segment is followed by a lateral segment on one side, then by a lateral segment on the other side, then by a second ventral segment, then by a second lateral segment on the first side, and so on. Each segment, by means of subsequent growth and cell-division, gives rise to a definite portion of the adult shoot. This may be designated a merophyte, as suggested by Douin (1925, p. 575), and the adult shoot in consequence is composed of three longitudinal rows of merophytes, two of which are lateral and the third ventral.

In the Paradoxae an important deviation from the course of development just described is met with. Although the apical cell in this group has three cutting faces, although two of these faces are lateral and one ven-

tral, and although the apical cell cuts off segments parallel with these faces, the segments do not arise in a spiral sequence but in what Goebel called a pendular sequence. In other words a ventral segment is followed by a lateral segment on one side, then by a second ventral segment, then by a lateral segment on the other side, then by a third ventral segment,

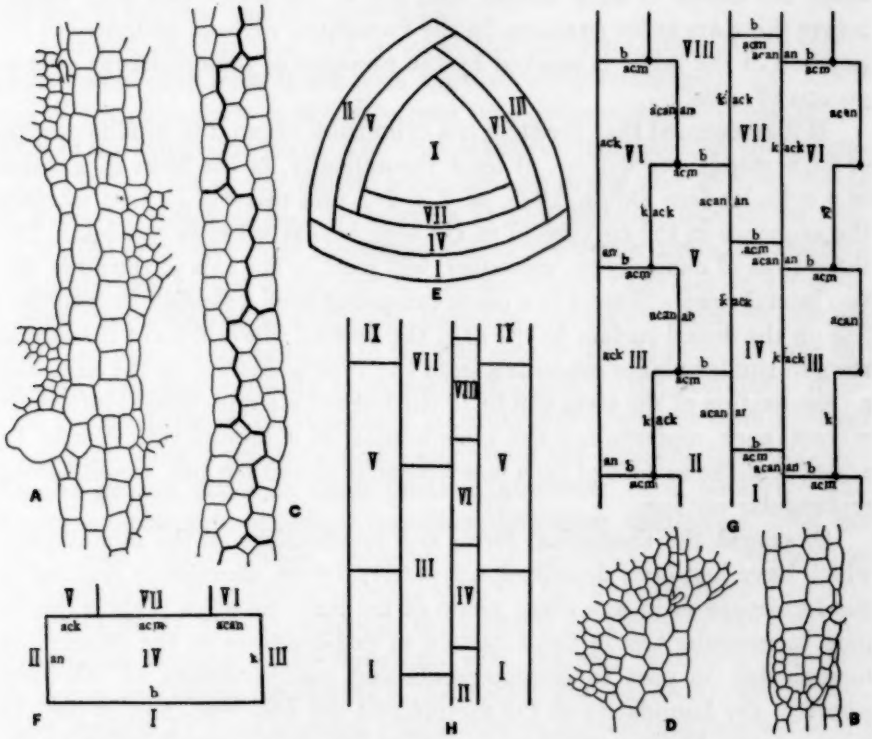


Fig. 8. A–D. *Lejeunea flava* (Swartz) Nees. A. Ventral view of stem, with underleaves dissected away, ×100. B. Lateral view of stem, showing attachment of a leaf, ×100. C. Dorsal view of stem, with leaves dissected away, ×100. D. Base of leaf, dorsal view, ×100. E–H. Diagrams. E. Apical cell and young segments cut off in a dextrorse spiral sequence. F. A single ventral segment. G. Superficial boundaries of merophytes in *L. flava*. H. Superficial boundaries of merophytes in *Aphanolejeunea microscopica* (Tayl.) Evans.

then by a second lateral segment on the first side, then by a fourth ventral segment, and so on. Goebel first associated the pendular sequence with the genus *Colura* (see 1915, p. 588), but it is found also in *Diplasiolejeunea* and *Cololejeunea*, as well as in the segregates from the latter genus (see Goebel, 1928, p. 26). In this type of development the merophytes are still arranged in three longitudinal rows, two of which are lateral and the third

ventral, but the ventral row has twice as many merophytes as either of the lateral rows.

Each lateral merophyte bears a leaf and each ventral merophyte an underleaf, if the species under consideration has underleaves. In the Hololstipae and Schizostipae, therefore, there are just as many underleaves as there are leaves in each lateral row, but in the Paradoxae with underleaves there are twice as many. In the Paradoxae without underleaves the position of the latter is marked by the presence of radicelliferous cells or groups of cells.

If it is assumed that the stem is a cylindrical organ, the cauline portion of each merophyte will be, at least theoretically, in the form of a sector of a cylinder (see Douin, 1925, *pl. 8, f. 18*), and this will be true whether the sequence in the cutting off of the segments is spiral or pendular. The three rows of merophytes, moreover, will meet in the axis of the stem, the two lateral rows will meet in a plane extending from a median longitudinal line on the dorsal surface to the axis, the ventral row will meet the lateral rows in similar planes extending from the ventral surface to the axis, and a cross-section of the stem will be in the form of a circle divided into three sectors, each representing the cross-section of a merophyte. It may be added that the surface of each merophyte, if spread out flat, would have a rectangular outline.

Of course the theoretical forms and relationships of the merophytes, which have just been described, are rarely, if ever, completely realized in the Lejeuneae or in any other group of the leafy hepatics. This is due in part to irregularities in the sequence of cell-divisions in the developing merophytes, in part to displacements and readjustments of cell-walls whereby the boundaries of the merophytes are obscured, and in part to other causes. At the same time a more or less close approximation to the theoretical condition can, in many cases, be demonstrated. This will become evident from the study of *Lejeunea flava* which may be considered representative of the Schizostipae.

Leitgeb's important studies on the leafy hepatics (1871, 1875) are of great help in interpreting the conditions found in *L. flava*. According to the nomenclature suggested by Nägeli and Leitgeb (see 1867, p. 77) each segment cut off from the apical cell is bounded by the following five walls: the free wall, the basiscopic wall, the kathodic wall, the acroscopic wall, and the anodic wall. In the accompanying diagram (fig. 8, E), which represents an apical cell (x) and a series of segments cut off in a dextrorse spiral sequence, the ventral segment IV may be taken as an illustrative example. For the sake of clearness this segment is represented also by itself (fig. 8, F) and it will be seen that the basiscopic wall (b) separates

the segment from segment I, the anodic wall (*an*) from segment II, the acroscopic wall from segments V, VII, and VI, and the kathodic wall (*k*) from segment III. Segment IV, therefore, is in contact with six other segments, and the merophyte developing from segment IV will be in close union with the merophytes developing from these segments, so far as their cauline portions are concerned. Of course the outline of the diagram represents the free wall of segment IV.

Although the free wall of a segment and the free surface of the merophyte developing from it are both approximately rectangular, the lower end of the merophyte is the only part that corresponds with one of the walls of the original segment. This was definitely demonstrated by Leitgeb (1871) in the case of the ventral segments and young ventral merophytes of *Radula complanata* (L.) Dumort., a species without underleaves. According to his account the basiscopic wall of the segment remains straight and gives rise to the lower end of the merophyte. The acroscopic wall, however, although at first straight, does not remain so, owing to changes that take place in the portions of the wall separating the segment from the two next younger segments. In segment IV (fig. 8, F) the portions in question are the kathodic portion (*ack*), separating the segment from segment V, and the anodic portion (*acan*), separating the segment from segment VI. As growth proceeds these portions gradually bend backward and finally assume a longitudinal direction, becoming continuous with the anodic and kathodic walls, respectively, of the segment. In this process the kathodic portion becomes longer than the anodic portion (as shown by Leitgeb's *pl. 11, f. 3 B*). Through the bending backward of the kathodic and anodic portions of the acroscopic wall, the only portion left to form the upper end of the merophyte is the median portion (*acm*), which separates segment IV from segment VII. It follows further that one side of the merophyte is derived from the anodic wall and the kathodic portion of the acroscopic wall of the segment, whereas the other side is derived from the kathodic wall and the anodic portion of the acroscopic wall. Since the free surface of the merophyte is rectangular the part derived from the kathodic wall must be longer than the part derived from the anodic wall.

The relationships demonstrated by Leitgeb in the ventral merophytes of *Radula complanata* are exhibited just as clearly in the ventral merophytes of *Lejeunea flava*, although each merophyte in the latter species bears an underleaf at the upper (or acroscopic) end. This is brought out by figure 8, A, which represents in ventral view a portion of a stem from which the underleaves have been dissected away. Since the spiral sequence in the selected example is dextrorse, the anodic sides of the merophytes are on the left and the kathodic sides on the right. The upper end of each ven-

tral merophyte is marked by a transverse band of four cells, indicating the place of attachment of an underleaf. Otherwise the merophyte is two cells wide, and it will be noted that the complete ventral merophyte figured is seven cells long on the left-hand side and eight cells long on the right-hand side. This indicates that the original peripheral cell of the very young merophyte (see Leitgeb, 1875, p. 5) undergoes one radial division and that this is followed by a series of three transverse divisions, the first giving rise to two cells in each row, the second to four, and the third (if complete) to eight. On the left-hand side of the merophyte figured one of the four cells formed by the second division failed to divide, so that only seven cells were formed. This seems to be the usual condition in the species under consideration.

The portion of the merophyte-boundary derived from the kathodic portion of the acroscopic wall extends from the group of four cells to the lobule on the left-hand side, and the portion derived from the anodic wall from the upper end of the lobule to the lower group of four cells. Similarly, the portion derived from the anodic portion of the acroscopic wall extends from the group of four cells to the lobule on the right-hand side, and the portion derived from the kathodic wall from the upper end of the lobule to the same group of cells. It will be seen at once that the portion derived from the kathodic portion of the acroscopic wall is much longer than that derived from the anodic portion and that the portion derived from the anodic wall is just as much shorter than that derived from the kathodic wall.

The conditions shown in figure 8, A, are illustrated diagrammatically in figure 8, G, which represents the surface of a stem rolled out to a plane. In this figure one series of lateral merophytes is repeated and two complete ventral merophytes, IV and VII, are shown. The same abbreviations are used as in figure 8, F, which represents segment IV prior to cell-division. It will be seen that *ack* in merophyte IV is longer than *acan* and that *an* is shorter than *k* by the same amount.

The free surfaces of the lateral merophytes in the leafy hepatics may deviate somewhat widely from the theoretical rectangular form. This is due in great part to the fact that the leaves are rarely transversely attached. If they are obliquely attached, as in species with distinctly incubous or succubous leaves, the free surface tends to be rhomboidal in form. This is clearly indicated in Buch's figure of *Cephalozia connivens* (1930, *f. 4, F*), in which the surfaces are shown to meet in a dorsal median line. The leaves in this species are succubous, and the upper end of each rhomboid, in consequence, forms an obtuse angle with the dorsal longitudinal side. If the leaves are complicate bilobed, as in *Radula* and the Lejeuneae,

another element of complexity is introduced. Leitgeb, fortunately, has given a careful description of the developing lateral merophytes in *Radula complanata*, and his account, in its more essential features, applies also to *Lejeunea flava*.

Each lateral segment in the *Radula*, according to Leitgeb's statements, divides in the usual way into two peripheral cells and an internal cell. The two peripheral cells bulge somewhat and the bulging portions represent the earliest rudiments of the lobe and lobule of the future leaf. As development proceeds the leaf-rudiment is cut off by walls, each of the two peripheral cells divides by a radial wall, and each of the four cells thus formed divides by a transverse wall. The cauline part of the young merophyte then consists of an acroscopic portion and a basiscopic portion, each composed of a transverse row of four cells (see Leitgeb, 1871, *pl. 12, f. 1, B* and *F*). The author goes on to show that the elongation of the merophyte takes place largely in the acroscopic portion, to which the leaf-rudiment is attached. During this process the line of attachment, which is slightly concave even at the beginning, becomes more sharply concave, and the mature lobe and lobule, in consequence, are almost longitudinally attached (1871, *pl. 11, f. 10 B*). Although Leitgeb does not indicate the boundaries of the mature lateral merophytes in *Radula complanata*, his description implies that their free surfaces meet in a dorsal median line and that the form of these surfaces is subrectangular.

In *Lejeunea flava* the presence of a dorsal row of cortical cells makes it evident that the free surfaces of the lateral merophytes do not meet in a median line. In other important respects, however, the merophytes agree with those of *Radula complanata*. The line of attachment of the leaves, for example, is essentially the same, as shown by figure 8, B, which represents the lateral view of a leaf-base. In this figure the two median rows of cells are lateral rows, the row on the left one of the ventral rows, and the row on the right the dorsal row. It will be seen that the line of attachment is strongly concave, that the lobe and lobule are almost longitudinally attached, and that four cells are present between the keel and the upper end of the lobe. These four cells indicate that the acroscopic portion of the young merophyte has taken part in the elongation of the stem, and that the original acroscopic cells have undergone a transverse division, followed by a second transverse division in each of the daughter-cells. But a comparison with figure 8, A, shows that four cells are present also in the lateral rows between the keels of the leaves and the lobules of the next older leaves on the same side. These four cells indicate that the basiscopic portion of the young merophyte has played an equally important part in the elongation of the stem, and that the original basiscopic cells have likewise under-

gone a series of two transverse divisions. It will be remembered that in *R. complanata* the predominant part in the elongation of the stem was played by the acroscopic portions of the young merophytes. Figure 8, B, shows further that the line of attachment of the lobe, throughout the greater part of its extent is on the outside of one of the lateral rows, whereas the line of attachment of the lobule is largely along the junction between the other lateral row and the adjoining ventral row. The same relationship is brought out in the cross-section of the stem of *L. flava*, shown in figure 6, L, as well as in some of the cross-sections of other species (see, for example, figure 6, H, left-side, and J).

An arrangement of the cortical cells in seven longitudinal rows, one of which is dorsal in position, is clearly shown by Leitgeb in two of his figures drawn from the northern *L. cavifolia* (Ehrh.) Lindb. (*L. serpyllifolia*), although he makes no mention of such an arrangement in his discussion of stem-structure in the leafy hepatics. These figures represent cross-sections, one (1875, *pl. 1, f. 1 B*) through a stem near the apical cell, the other (1875, *pl. 1, f. 8*) through the base of a young branch. Both figures show seven cortical cells, one of which is dorsal, but the first shows five medullary cells, whereas the second shows only three. The latter is essentially like the writer's figures of *Microlejeunea bullata* (fig. 6, N) and *Leptolejeunea elliptica* (fig. 6, P).

Although the writer has not studied the development of the merophytes in *L. flava*, it seems probable that the dorsal row of cortical cells is derived from both rows of lateral merophytes, a view first suggested by Dr. Hempstead Castle. If this view is correct each merophyte would pursue the normal course of development until the separation of the acroscopic portion from the basiscopic portion by means of transverse walls. At this stage each portion would have two peripheral cells side by side. The more dorsal cell in the acroscopic portion would then divide by a radial wall, but the corresponding cell in the basiscopic portion would undergo no such division. The succeeding transverse walls would divide each of the original cells into four cells, as already noted; and, as a result, the acroscopic portion of the merophyte would show three rows of cortical cells, each composed of four cells, whereas the basiscopic portion would show only two such rows. Since the cortical cells are approximately equal, and since the junction between the ventral side of a merophyte and the ventral merophytes is a straight line, as shown in figure 8, A, the extra row of cortical cells would necessarily project on the dorsal side. The extra rows in the lateral merophytes on the other side of the stem would project in the same way on the dorsal side and occupy the spaces between the projecting por-

tions of the merophytes on the first side. In this way the continuous dorsal row of cortical cells would be formed.

The conditions found in the stem of *Lejeunea flava* support the course of development just outlined. Figure 8, C, represents the upper surface of a stem from which the leaves have been dissected away and on which the boundaries of the merophytes are indicated by heavier lines. It will be seen that each merophyte shows four cells belonging to the dorsal row and eight cells to one of the lateral rows; the eight cells belonging to the other lateral row are not visible. At the upper end of each merophyte a small diamond-shaped cell at the junction of a leaf with the stem is indicated. The line of attachment of the lobe begins at the dorsal end of this cell, that is from about the middle of the dorsal row, extends along the upper end of the merophyte, and then downward along the side of the stem for a distance of four cells. The attachment of the lobe to a cell of the dorsal row is shown in figure 8, D, which represents the base of a lobe. It will be seen that the rounded basal cell with a papilla lies directly over the dorsal cell to which it is attached. The cell at the left of this rounded cell partially conceals the diamond-shaped cell described above. The fact that the leaves are attached to cells of the dorsal row is a further indication that this row is derived from lateral merophytes.

In the diagrammatic figure 8, E, it is shown that the kathodic portion of the acroscopic wall of one segment is the same as the kathodic wall of the first succeeding segment, and that the anodic portion is the same as the anodic wall of the second succeeding segment. In segment IV, for example, *ack* is the same as *k* in segment V, and *acan* the same as *an* in segment VI. The figure indicates further that *ack* of segment I forms an angle with *acan* of segment II, that the latter forms an angle with *ack* of segment IV, and so on. It follows from this that the kathodic and anodic portions of the acroscopic walls of the segments in two adjoining rows form a zigzag line extending from an angle of the diagram to the corresponding angle of the apical cell.

The diagrammatic figure 8, G, brings out the relationships, not only between the ventral and lateral merophytes but also between the two rows of lateral merophytes, so far as their free surfaces are concerned. The figure indicates also that the kathodic and anodic portions of the acroscopic walls of the lateral segments bend backward in the way described for the ventral segments. In this way the zigzag lines shown in figure 8, E, have become continuous longitudinal lines (see, in this connection Nägeli & Leitgeb, 1867, *p. 78, pl. 11, f. 3*) or, in the case of the zigzag line between the two rows of lateral segments, an alternating series of short longitudinal

lines, connected by shorter transverse lines. It may be further noted that in each lateral merophyte, just as in each ventral merophyte, *ack* is longer than *acan*.

Although the leaves and underleaves of *Lejeunea flava* and of most other leafy hepatics are arranged in a continuous spiral, the leaves are evenly spaced along the stem. In other words each leaf on one side of the stem is midway between two leaves on the opposite side. This signifies that the leaves and underleaves do not occur at equal intervals along the spiral, although the leaves themselves do so. If the spiral is dextrorse a complete half-turn of the spiral on the dorsal surface of the stem is taken up in passing from a leaf on one side to the next higher leaf on the other side, but the following half-turn on the ventral side would include an underleaf. It follows that the underleaf between two leaves in the spiral is closer to the leaves than these are to each other.

This relationship, also, is brought out by figure 8, G. It will be seen that the ventral merophyte IV is in contact with merophytes II and V on the left-hand side and with merophytes III and VI on the right-hand side, and that it is included between merophytes III and V in a ventral half-turn of the spiral. If it is assumed that the upper end of each merophyte, *acm*, indicates the line of attachment of a leaf or underleaf (or, in the case of the lateral merophytes, the upper limit of the line of attachment), *acan* in merophyte IV would represent the distance from the underleaf of that merophyte to the leaf of merophyte III and *acan* in merophyte V the distance from the same underleaf to the leaf of merophyte V. It will be seen that each of these distances is less than *acan* in merophyte III, which represents the distance between the leaf of merophyte III and the leaf of merophyte II. In fact *acan* in merophyte III is equal to *acan* in merophyte IV plus *acan* in merophyte V. The distribution of the leaves and underleaves at unequal intervals along the spiral represents a mechanism whereby the leaves are advantageously placed with reference to the rays of light.

It is safe to assume that the merophytes of the other Lejeuneae with seven rows of cortical cells are similar to those of *Lejeunea flava*. This is true, not only of species belonging to Schizostipae and Holostipae, but also of those belonging to the Paradoxae with underleaves, except that in the last group the ventral merophytes are only half as long as the lateral merophytes. The diagrammatic figure 8, G, therefore, would illustrate the condition found in these Paradoxae, if each ventral merophyte were divided by a median transverse line. In the still more simplified Paradoxae without underleaves the lateral merophytes clearly meet in a median longitudinal line on the dorsal surface of the stem, and this indicates that they are no broader in the acroscopic than in the basiscopic portion. The dia-

grammatic Fig. 8, H, based on *Aphanolejeunea microscopica*, represents the boundaries of the merophytes in such forms, and one row of lateral merophytes is repeated, just as in figure 8, G. It will be seen that the ventral merophytes are half the length of the lateral merophytes, that the latter are of the same width throughout, that each ventral merophyte is in contact with five other merophytes, and that each lateral merophyte is in contact with seven. It will be seen further that, although the acroscopic walls of the lateral segments have bent back on each side, the corresponding walls of the ventral segments have bent back on only one side.

No attempt has been made to map out the merophytes in Lejeuneae with more than seven rows of cortical cells. In the more complex forms belonging to this category, such as *Bryopteris filicina* (fig. 1) and *Ptychanthus striatus* (fig. 2), the cortical cells are in many rows and the rows are irregular, making it difficult to determine whether the lateral merophytes meet in a dorsal median line or not. But in some of the less complex forms, such as *Dicranolejeunea axillaris* (fig. 5, B) and *Odontolejeunea lunulata* (fig. 5, D), the rows of cortical cells are fewer and more regular, and a median dorsal row can be distinguished. It is evident that the lateral merophytes of such forms agree with those of *Lejeunea flava* in being broader in the acroscopic than in the basiscopic portion.

So far as the writer knows lateral merophytes of the type found in *L. flava* have not previously been recorded in the hepatics. Leitgeb, however, many years ago, described and figured similar merophytes in two mosses, *Fontinalis antipyretica* L. and *Sphagnum cuspidatum* Ehrh. In the *Fontinalis* (1868, *pl. 11, f. 7*) the acroscopic portion projects beyond the basiscopic on both sides; in the *Sphagnum* (1869, *pl. 8, f. 1*) on the anodic side only. The merophytes of the *Sphagnum* are thus similar to the lateral merophytes of *Lejeunea flava*, except that in the latter species the projecting portion of each merophyte is on the anodic side in one row of lateral merophytes and on the kathodic side in the other. This difference is clearly associated with the fact that the shoots of the *Lejeunea* are bilateral, whereas those of the *Sphagnum* are radial. The two rows of leaves in the *Lejeunea*, therefore, together with the merophytes of which they form parts, are symmetrically placed with respect to a vertical plane. The five rows of leaves in the *Sphagnum*, on the contrary, are arranged at equal intervals along a continuous spiral, without reference to any one longitudinal plane.

The boundaries of the merophytes inside the medulla may now be briefly considered. It has already been noted that these are theoretically in the form of longitudinal planes meeting in the axis of the stem and that they should appear in a cross-section as three converging lines. The cross-

section of *L. flava* (fig. 6, L) shows, however, that only zigzag lines are present, and that it is difficult to decide positively which of these zigzag lines represent the boundaries. In all probability the ventral group of four cells belongs to the ventral merophyte, the dorsilateral group of five cells on the right to the lateral merophyte showing three cortical cells (distinguishable by the attached lobe and lobule), and the dorsilateral group of four cells on the left to the lateral merophyte showing two cortical cells; but there is nothing except their position to distinguish the zigzag lines separating these groups of cells from other zigzag lines. In Lejeuneae with more complex medullae than that of *L. flava* the difficulties of distinguishing the boundaries are increased, as is evident from the cross-sections of such forms as *Taxilejeunea pterogonia* (fig. 6, B), *Neurolejeunea Breutelii* (fig. 3, C) and *Brachiolejeunea insularis* (fig. 5, A). It is only in the highly simplified species with but three rows of medullary cells, such as *Microlejeunea bullata* (fig. 6, N) and *Diplasiolejeunea unidentata* (fig. 7, B), that the boundaries between the merophytes in the medulla are actually straight lines. Here there is no question that each row of merophytes has a single row of medullary cells. The fact that the still more simplified Paradoxae without underleaves have only one row of medullary cells would seem to indicate that the ventral segments in these forms were the only ones that cut off internal cells. In accordance with this idea each merophyte in such a stem as that of *Aphanolejeunea microscopica* (fig. 7, F) would be composed of only two rows of cells, the ventral merophyte of one medullary and one cortical row, and each lateral merophyte of two cortical rows.

MATERIAL EXAMINED

The stem-structure of thirty-five species of the Lejeuneae, representing twenty-nine genera, is discussed in the preceding pages. The descriptions and figures of these various species have been drawn from the following specimens: *Anoplolejeunea conferta*, near the Finca Sepacuite, Guatemala, *O. F. Cook and R. F. Griggs*, 1902, No. 190; *Aphanolejeunea microscopica*, Ballachulich, Argyllshire, Scotland, *S. M. Macvicar*, 1904; *Archilejeunea Spruceana*, near Bartica, British Guiana, *P. W. Richards*, 1929, No. 201; *Brachiolejeunea insularis*, near Castleton Botanical Garden, Jamaica, *L. M. Underwood*, 1903, No. 55; *Bryopteris filicina*, Old England Falls, Jamaica, *L. M. Underwood*, 1903, No. XX; *Caudalejeunea Lehmanniana*, Hattie Bauer Hammock, Florida, *J. K. Small and C. A. Mosier*, 1915, No. 5301; *Colura ornata*, Mt. Salak, Java, *V. Schiffner*, 1893, distributed in Fr. Verdoorn, Hep. Select. et Crit., No. 151; *Cyclolejeunea chitonia*, El Yunque, Porto Rico, *A. W. Evans*, 1902, No. 82; *C. convexistipa*, Mora Forest, east of Sangre Grande, Trinidad, *E. G. Britton*, No. 2871a; *C. peruviana*,

Aripo Savanna, Trinidad, *R. Thaxter*, 1913; *Cystolejeunea lineata*, El Yunque, Porto Rico, *A. W. Evans*, 1902, No. 46 in part; *Dicranolejeunea axillaris*, Ecuador, *R. Spruce*, distributed in Hep. Spruceanae; *Diplasiolejeunea pellucida*, John Crow Peak, Jamaica, *A. W. Evans*, 1903, No.135 in part; *D. unidentata*, Mansfield, near Bath, Jamaica, *A. W. Evans*, 1903, No. 336; *Drepanolejeunea inchoata*, El Yunque, Porto Rico, *A. W. Evans*, 1902, No. 117; *Euosmolejeunea trifaria*, Mansfield, near Bath, Jamaica, *A. W. Evans*, 1903, No. 341; *Hygrolejeunea cerina*, Banao Hills, Santa Clara, Cuba, *Brother Clement*, 1915, No. 25; *Lejeunea flava*, Chinchona, Jamaica, *A. W. Evans*, 1906, No. 409; *L. inundata*, near Bartica, British Guiana, *P. W. Richards*, 1929, No. 365; *Leptocolea planifolia*, Utuado, Porto Rico, *M. A. Howe*, 1906, No. 862 in part; *L. scabriflora*, Sulphur River, Bath, Jamaica, *A. W. Evans*, 1903, No. 322b; *Leptolejeunea elliptica*, Green River Valley, Jamaica, *A. W. Evans*, 1903, No. 212 in part; *Leucolejeunea xanthocarpa*, Indefatigable Island, Galapagos Islands, *J. T. Howell*, 1932, No. 257 in part; *Mastigolejeunea auriculata*, Eustis, Florida, *L. M. Underwood*, 1891, No. 84; *Microlejeunea bullata*, Sanford, Florida, *S. Rapp*, 1913, No. 78; *Neurolejeunea Breutelii*, trail to Vinegar Hill, Jamaica, *A. W. Evans*, 1906, No. 453, distributed in C. C. Haynes, Amer. Hep. No. 65; *Odontolejeunea lunulata*, near Bartica, British Guiana, *P. W. Richards*, 1929, No. 492; *Omphalanthus filiformis*, near Hardware Gap, Jamaica, *A. W. Evans*, 1903, No. 183; *Potamolejeunea orinocensis* Steph., near Bartica, British Guiana, 1929, *P. W. Richards*, No. 367; *Ptychanthus striatus*, Mt. Singalang, Sumatra, *V. Schiffner*, 1894, distributed in Fr. Verdoorn, Hep. Select. et Crit., No. 264; *Pycnolejeunea macroloba*, near Bartica, British Guiana, *P. W. Richards*, 1929, No 443a; *Stictolejeunea Kunzeana*, Chimborazo, Ecuador, *R. Spruce*, distributed in Hep. Spruceanae; *S. squamata*, Troy, Jamaica, *A. W. Evans*, 1906, No. 678; *Taxilejeunea pterogonia*, San Miguel, Urubamba Valley, Peru, *O. F. Cook and G. B. Gilbert*, 1915, No. 1180; *Thysananthus amazonicus*, near Bartica, British Guiana, *P. W. Richards*, 1929, No. 188.

SUMMARY

The stems of the Lejeuneae show a differentiation into a medulla and a unistratose cortex, the cells of which are arranged in more or less distinct longitudinal rows.

The medullary cells, with few exceptions, are more than twice the length of the cortical cells but have a smaller diameter.

The stems of the Holostipae, as a rule, are more complexly organized than those of the Schizostipae and Paradoxae, and the last named group includes the most simply organized stems of all.

The highest degree of differentiation is found in the horizontally spreading secondary stems of certain Holostipae, in which a distinct skeletal tissue composed of fiber-like cells is developed at the periphery of the medulla.

In stems of this character the medulla is sixteen to twenty cells thick from top to bottom, and the number of rows of cortical cells may be as high as seventy.

In passing from the more complex Holostipae to the less complex the rows of cortical cells become fewer and fewer, reaching a limit of seven rows in a few cases.

In the Schizostipae, with few exceptions, the cortical cells are definitely in seven longitudinal rows, one of which is dorsal in position, two on each side lateral, and two ventral.

In the Paradoxae with underleaves the cortical cells have the same arrangement as in the majority of the Schizostipae; in the Paradoxae without underleaves, however, the cortical cells are in only five or six rows, two of which on each side are lateral in position and the remaining one or two ventral.

In passing from the most complex Holostipae to the simplest Paradoxae the medulla becomes more and more reduced, reaching a limit in the Paradoxae without underleaves, in which only one row of medullary cells is present.

From the standpoint of evolution the more primitive types of stems in the Lejeuneae are apparently those found in certain Holostipae.

From stems of this character two lines of advance may perhaps be recognized, one leading to greater complexity and the other to simplification and reduction, culminating in the Paradoxae without underleaves.

The cortical cells in the stems of the Lejeuneae, especially if their cavities are large, may play a part in the storage of water, as well as in the processes of absorption and photosynthesis.

Thick cell-walls in either cortex or medulla form a part of the skeletal system of the plant but may be even more important on account of their power of imbibing water rapidly.

The adult shoot in the Lejeuneae is made up of two rows of lateral merophytes and one row of ventral merophytes, each merophyte being derived from one of the segments cut off from the apical cell.

Each merophyte consists of a leaf or underleaf and of a portion of the stem, which is theoretically in the form of a sector of a cylinder.

In the more complex types of stem, with numerous rows of cortical cells, the superficial boundaries of the merophytes are indistinct; but in

stems with seven rows of cortical cells, or fewer, the superficial boundaries are more definite.

In *Lejeunea flava*, which may be considered typical of forms with seven rows, the ventral merophytes are two cells in width by about eight cells in length and are separated from the lateral merophytes by approximately straight lines.

The lateral merophytes, however, which are also about eight cells long, are three cells wide in the upper half and only two cells wide in the lower half.

The extra rows in the upper halves of successive merophytes are continuous with one another and form the dorsal row of cortical cells, which is therefore derived from both rows of lateral segments.

The rows of lateral merophytes, in consequence, instead of being separated from one another by a straight line, are separated by a series of short longitudinal lines of equal length connected by shorter transverse lines.

In the Paradoxae without underleaves, typified by *Aphanolejeunea microscopica*, the lateral merophytes are two cells wide throughout and are separated from one another by a straight line.

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The Oedogoniaceae of Oklahoma including new species and varieties[1]

CLARENCE E. TAFT

(WITH PLATES 15 AND 16)

During the past two years the writer has carried on a survey of the algae of Oklahoma based on approximately four hundred collections made during the spring of 1932 and the summer of 1933. As a partial result of this survey, sixty-four species and varieties of the two genera, *Bulbochaete* and *Oedogonium*, have been recorded. Of this number ten are new to science, while one formerly regarded as a form has been given varietal rank, and two others have been returned to varietal rank. Exclusive of those newly described, six are new records for the United States and are indicated as such by an asterisk. In addition, critical notes have been added wherever the material differed enough to justify such an addition.

With but one exception, that of *Oe. exocostatum* which appeared in the late summer, all species listed were found in fruiting condition in collections dating from May 1 to May 15, 1932.

Although the collections were representative of the entire state, the range of distribution of these two genera is quite limited, coinciding closely with the shale and sandstone mountain areas along the eastern border. While present in small numbers they never formed a conspicuous group in the prairie regions, a fact which also was true of the granite and limestone mountains in the southwestern part of the state.

The genus *Oedocladium* has not been recorded from Oklahoma.

Acknowledgement is due Dr. L. H. Tiffany of the Department of Botany of this University for his kindness in checking the new species, and for his helpful suggestions and criticisms throughout the preparation of the report. Also to Mrs. Taft, through whose efforts the spore drawings were made possible.

BULBOCHAETE Agardh.

1. **B. alpina** sp. nov. (figs. 5 and 6).

B. dioica, nannandria, idioandrospora; oogoniis depresso-globosis, pantentibus, sub setis terminalibus setis; oosporis eadem forma ac oogoniis, mesosporio scrobiculis angulare ornato, seriebus scrobiculorum; dissepimento cellularum suffultoriarum fere mediano; androsporangiis epigynis, 1–3 cellularibus; nannandribus in oogoniis sedentibus, antheridio exteriore, stipite curvato, unicellulari; cell. veget. 20–30×53–106μ; oogon. 59×53–56μ; oospor. 58×51–54μ; cell. androsp. 17–20×13–17μ; stip. nannandr. 10–11×36–46μ; cell. antherid. 10–11×15–17μ.

[1] Contributions from Department of Botany, Ohio State Univ. No. 343.

Dioecious, nannandrous, idioandrosporous, oogonium depressed globose, patent, below the terminal setae; oospore of the same form as the oogonium, middle spore wall scrobiculate, pits angular, concentrically arranged; division of the suffultory cell median; androsporangium 1–3, epigynous; dwarf male on the oogonium, curved, antheridium 1, exterior; vegetative cell 20–30×53–106μ; oogonium 59×53–56μ; oospore 58×51–54μ; androsporangium 17–20×13–17μ; dwarf male stripe 10–11×36–46μ; antheridium 10–11×15–17μ.

Herb. C.E.T. 310.

This species is characterized by a scrobiculate oospore in which the pits are angular. In size it is to be compared to *B. gigantea*.

2. **B. areolata** sp. nov. (figs. 7 and 8).

B. dioica, nannandria, gynandrospora; oogoniis ellipsoideis, patentibus vel erectis, sub androsporangiis vel setis terminalibus vel sub cellulis vegetativis, androsporangiis feris setis; oosporis ellipsoideis, episporio oosporae profunde areolato (in sectione optica profunde undulato); dissepimento cellularum suffultoriarum supremus; androsporangiis 4-cellulariabus, epigynis; nannandribus paullum curvatis, in cellulis vegetativis sedentibus, antheridio exteriore, 1–3 cellulari; cell. veget. 15–20×20–46μ; oogon. 33–36×53–63μ; oospor. 31–35×52–59μ; cell. androsp. 20–26×17–23μ; stip. nannandr. 13–15 ×23–25μ; cell. antherid. 7–10×4–7μ.

Dioecious, nannandrous, gynandrosporous; oogonium ellipsoid, patent to erect, below the androsporangia, terminal setae, or vegetative cells; oospore ellipsoid, outer spore wall deeply areolate with sharp points at the angles of the areolations (in section deeply undulate); division of the suffultory cell supreme; androsporangium 1–4, epigynous; dwarf male slightly curved, on the vegetative cells, antheridium 1–3, exterior.

Vegetative cell 15–20×20–46μ; oogonium 33–36×53–63μ; oospore 31–35 ×52–59μ; androsporangium 20–26×17–23μ; dwarf male stipe 13–15×23–25μ; antheridium 7–10×4–7μ.

Herb. C.E.T. 312.

This species is characterized by the deeply areolate outer spore wall, a type of spore marking which is not found anywhere else in the genus *Bulbochaete*.

3. *B. crassiuscula* Nordst.

4. *B. crenulata* Pringsheim

5. **B. cimarronea** sp. nov. (figs. 1 and 2).

B. dioica, nannandria, gynandrospora; oogoniis ellipsoideis, patentibus, sub setis terminalibus vel rarissime sub cellulis vegetativis setis; oosporis ellipsoideis, costis episporii oosporarum, ut videtur, glabris, non crenatis; dissepimento cellularum suffultoriarum supremus; androsporangiis epigynis, 1–2 cellularibus; nannandribus in cellulis vegetativis, raro in oogoniis ipsis sedentibus, antheridio exteriore, 1–2 cellulari; cell. veget. 14–17×17–23μ;

oogon. 26–29×36–39μ; oospor. 24–26×35–37μ; cell. androsp. 10–11×5–7μ; stip. nannandr. 13–17×20–23μ; cell. antherid. 7–8×5–7μ.

Dioecious, nannandrous, gynandrosporous, oogonium ellipsoid, patent, below the terminal setae or rarely below the vegetative cells; oospore ellipsoid, outer spore wall longitudinally ribbed, ribs entire; division of the suffultory cell supreme; androsporangium 1–2, epigynous, dwarf male located on vegetative cell, rarely on the oogonium, antheridium 1–2, exterior; vegetative cell 14–17×17–23μ; oogonium 26–29×36–39μ; oospore 24–26×35–37μ; androsporangium 10–11×5–7μ; dwarf male stipe 13–17×20–23μ; antheridium 7–8×5–7μ.

Herb. C.E.T. 163.

This species is among the smallest known forms combining the characters of the ellipsoid oogonium and longitudinally ribbed, ellipsoid spore. It is to be compared with *B. pygmaea* from which it differs by the presence of a divided suffultory cell, and the entire ridges of the oospore.

6. **B. Furberae** Collins **var. depressa** var. nov. (figs. 3 and 4).

Ogoniis sub setis terminalibus vel rarius sub cellulis suffultoris setis; androsporangiis 1–3 cellularibus, epigynis; nannandribus in oogoniis vel prope ea sedentibus, antheridio interiore, stipite paullum curvato; cell. veget. 13–17×33–83μ; oogon. 46–50×35–37μ; oospor. 44–48×32–35μ; cell. androsp. 11–14×6–10μ; nannandr. 10–12×26–30μ. Certerum ut in typo.

Oogonium terminal (rarely below the suffultory cell); androsporangium 1–3, epigynous; dwarf males curved, on or near the oogonia, antheridium interior; vegetative cell 13–17×33–83μ; oogonium 46–50×35–37μ; oospore 44–48×32–35μ; androsporangium 11–14×6–10μ; dwarf male 10–12×26–30μ.

Herb. C.E.T. 312.

This variety differs from the type in the larger size of the reproductive structures. It should be compared to *B. brebissonii* in which the division of the suffultory cell is basal.

7. *B. gigantea* Pringsheim
8. *B. intermedia* De Bary
*9. *B. minuta* West and West
*10. *B. nana* Wittr.

Oogonia and oospores slightly broader and longer; oogonium 26–30×36–42μ; oospore 25–28×35–41μ.

11. *B. Nordstedtii* Wittr.
12. *B. obliqua* Lundell

The oogonia and oospores were narrower than in the type; oogonium 50–53×43–46μ; oospore 49–51×42–45μ.

13. *B. rectangularis* Wittr.
14. *B. rectangularis* Wittr. var. *hiloensis* Nordst.

Vegetative cell 16–20×26–33μ; oogonium 29–33×43–49μ; oospore 26–30×38–45μ; androsporangium 13–17×13–15μ; dwarf male stipe 13–17×23–27μ; antheridium 8–9×5–7μ.

The original dimensions of this variety have been rewritten so as to include the slight variations of the Oklahoma material.

15. *B. repanda* Wittr.

Oedogonium Link

1. *Oe. armigerum* Hirn

Vegetative cell 9–13×36–100μ; oogonium 29–33×30–35μ; oospore 26–30×26–29μ; dwarf male, lower cell 7–8×20–24μ, upper cell 4–6×21–30μ; antheridium 5–6×7–8μ.

This description combines the original dimensions with those of the Oklahoma material.

2. *Oe. aster* Wittr.

Vegetative cell 7–13×50–110μ; oogonium 33–37×(27–)30–39μ; oospore 29–32×25–30μ; dwarf male stipe 6–7×20–25μ; antheridium 5–6×7–8μ.

These are the original dimensions combined with those of the Oklahoma material.

3. *Oe. bohemicum* Hirn
4. *Oe. borisianum* (Le Cl.) Wittr.
5. *Oe. Boscii* (Le Cl.) Wittr. var. *occidentale* Hirn

Vegetative cell 8–16×50–165μ; oogonium 29–38×69–100μ; oospore 29–37×42–50μ; antheridium 12–13×10–16μ.

These are a combination of the original and the Oklahoma dimensions.

6. *Oe. Braunii* Kuetz.
7. *Oe. capitellatum* Wittr.
8. *Oe. cardiacum* (Hass.) Wittr.
9. *Oe. cardiacum* (Hass.) Wittr. var. *carbonicum* Wittr.

In this variety the oospore was smaller, being 36–40×39–43μ instead of 40–52×46–65μ.

10. *Oe. cardiacum* (Hass.) Wittr. var. *minus* Lemmerman

The oogonium and oospore were slightly larger. Oogonium 46–50×43–59μ; oospore 40–43×40–42μ.

11. *Oe. concatenatum* (Hass.) Wittr.
12. **Oe. concatenatum** (Hass.) Wittr. **var. regulare** var. nov. (fig. 20).

Oogoniis singulis, suboviformibus vel quadrangulari ellipsoidies; oosporiis eadem forma ac oogoniis, mesosporio scrobiculato, seriebus scrobiculorum; cell. veget. 23–26×89–142μ; cell. suffult. 53–59×105μ; oogon. 66–69×99–106μ; oospor. 63–68×83–86μ; cell. androsp. 32×32μ; stip. nannandr. 16–20×57–70μ; cell. antherid. 12–15×8–16μ. Certerum ut in typo.

Oogonium single, subovoid to quadrangularly-ellipsoid; oospore of the same form as the oogonium, median spore wall scrobiculate, scrobiculations concentrically arranged. Vegetative cell 23–26×89–142μ; suffultory cell 53–59 ×105μ; oogonium 66–69×99–106μ; oospore 63–68×83–86μ androsporangium 32×32μ; dwarf male stipe 16–20×57–70μ; antheridium 12–15×8–16μ.

Herb. C.E.T. 196.

In *Oe. concatenatum* the pits of the median spore wall are arranged in longitudinal series, while in this variety they are arranged concentrically. Furthermore the subovoid to quadrangularly-ellipsoid spore readily separates it from the variety *hutchensiae* (Wittr.) Hirn whose spores are nearly globose.

13. *Oe. crassiusculum* Wittr.

14. *Oe. crassiusculum* Wittr. var. *arechavaletae* (Wittr.) Hirn

The diameter of the vegetative cells of the Oklahoma material was greater than that of the type. Vegetative cell 33–35×66–108μ. This variety is idioandrosporous.

15. *Oe. crassiusculum* Wittr. var. *cataractum* (Wolle) Tiffany

16. *Oe. crassiusculum* Wittr. var. *idioandrosporum* Nordst. and Wittr.

17. *Oe. crassum* (Hass.) Wittr.

18. *Oe. crispum* (Hass.) Wittr.

19. *Oe. crispum* (Hass.) Wittr. var. *gracilescens* Wittr.

20. *Oe. crispum* (Hass.) Wittr. var. *granulosum* Nordst.

[*Oe. crispum* (Hass.) Wittr. f. *granulosum* (Nordst.) Hirn]

Oogonium subglobose to obovoid-globose, almost completely filled by the oospore; antheridium subepigynous or hypogynous; wall of oospore punctate-granulate; vegetative cell 13–17×29–63μ; oogonium 36–43×42–46μ; oospore 34–40×34–40μ; antheridium 8–13×7–11μ. Otherwise as in the type.

Herb. C.E.T. 56.

21. *Oe. cryptoporum* Wittr.

22. *Oe. cryptoporum* Wittr. var. *vulgare* Wittr.

23. *Oe. cyathigerum* Wittr.

24. *Oe. cyathigerum* Wittr. var. *ellipticum* Magnus and Wille

Gynandrosporous; vegetative cell 19–30×30–132μ; suffultory cell 26–46 ×40–125μ; oogonium 50–66×(59–) 68–94μ; oospore 48–65×45–66 (–73)μ; androsporangium 1–6, 23–26×14–19μ; dwarf male stipe 13–18×43–59μ.

These dimensions combine the original with those of the Oklahoma material. The androsporangia are described for the first time.

25. *Oe. echinospermum* Al. Br.

26. *Oe. exocostatum* Tiffany

27. **Oe. flavescens** (Hass.) Wittr. **var. minus** var. nov. (figs. 10, 11, 12).

Idioandrosporum; poro mediano vel infra medium apertis; oosporiis globosis vel sub-globosis; androsporangiis 1–3 cellularibus; antheridio exteriore, uni-cellulari; cell. veget. 16–20×62–112μ; oogon. 39–46×46–50μ; oospor. 36–43×36–43μ; cell. androsp. 16–23×10–20μ; stip. nannandr. 10–13×33–45μ; cell. antherid. 8–10×7–13μ. Certerum ut in typo.

Idioandrosporous; pore median to inframedian; oospore globose to subglobose; androsporangium 1–3; antheridium 1, exterior; vegetative cell 16–20 ×62–112μ; oogonium 49–46×46–50μ; oospore 36–43×36–43μ; androsporangium 16–23×10–20μ; dwarf male stipe 10–13×33–45μ; antheridium 8–10 ×7–13μ.

Herb. C.E.T. 53.

The variety *minus* closely resembles the type except in its smaller size. This along with the inframedian position of the pore and the subglobose oospore, both of which are commonly present, give this form varietal rank.

28. **Oe. fuscum** sp. nov. (figs. 13, 14 and 15).

Oe. dioicum, nannandrium, gynandrosporum; oogoniis singulis, ellipsoideis vel ellipsoideo-globosis vel globosis, poro mediano vel infra medium apertis; oosporiis ellipsoideo-globosis vel globosis; oogoniis complentibus vel non complentibus; episporio reticulato-verrucoso, fusco; cellulis suffultoriis tumidis; androsporangiis ?–3 cellularibus, epigynis; nannandribus paullum curvatis, in cellulis suffultoriis sedentibus, antheridio exteriore, 1–2 cellulari; cell. veget. 10–17×33–73μ; cell. suffult. 23–27×50–53μ; oogon. 36–43×46–56μ; oospor. 34–40×42–46μ; cell. androsp. 10–11×7–10μ; stip. nannandr. 7–9×20–23μ; cell. antherid. 6–7×5–7μ.

Dioecious, nannandrous, gynandrosporous, oogonium single, ellipsoid to ellipsoid-globose to globose, pore median to inframedian; oospore ellipsoid-globose to globose, completely filling or not completely filling the oogonium; outer spore wall reticulate-verrucose, brown; suffultory cell enlarged; androsporangium ?–3, epigynous; dwarf male slightly curved, on suffultory cell, antheridium 1–2, exterior; vegetative cell 10–17×33–73μ; suffultory cell 23–27×50–53μ; oogonium 36–43×46–56μ; oospore 34–40×42–46μ; androsporangium 10–11×7–10μ; dwarf male stipe 7–9×20–23μ; antheridium 6–7 ×5–7μ.

Herb. C.E.T. 305.

Due to the reticulate-verrucose outer spore wall, this species occupies a unique position in the genus *Oedogonium*, and may be readily separated from all the known species by this one character.

29. *Oe. giganteum* Kuetz.; Wittr.

The diameter of the vegetative cells of this species was slightly greater, being 49–53μ instead of 30–50μ.

30. *Oe. grande* Kuetz.; Wittr.

31. *Oe. grande* Kuetz.; Wittr. var. *angustum* Hirn

32. *Oe. Gunnii* Wittr.

*33. *Oe. Howardii* G. S. West

Vegetative cell 9–13×23–43μ; oogonium 26–31×23-30μ; oospore 20–27×20–27μ.

Part of the Oklahoma material was typical of *Oe. Howardii*, while in the same collections some filaments had smaller oogonia and oospores. Based on this material as well as that from Puerto Rico recently examined by Dr. L. H. Tiffany, *Oe. Howardii* and its variety *minus* are not easily separable.

34. **Oe. illinoisense** Transeau **var. oklahomense** var. nov. (figs. 24–26).

(?) Idioandrosporum; costis spiralibus numero 4–6, non utrinque in polo; cellula fili basali forma, ut vulgo, elongata; (?) androsporangiis; antheridio exteriore unicellulari; cell. veget. 10–20×73–125μ; cell. suffult. 26–34×69–75μ; oogon. 49–56×60–65μ; oospor. 43–46×43–46μ; stip. nannandr. 11–13×38–46μ; cell. antherid. 7–9×12–13μ. Certerum ut in typo.

(?) Idioandrosporous; outer spore wall with 4–6 spiral ribs, not united at the poles; basal cell elongate; (?) androsporangium; antheridium 1, exterior; vegetative cell 10–20×73–125μ; suffultory cell 26–34×69–75μ; oogonium 49–56×60–65μ; oospore 43–46×43–46μ; dwarf male stipe 11–13×38–46μ; antheridium 7–9×12–13μ.

Herb. C.E.T. 240.

In general appearance this variety resembles the species, but differs in its smaller size and by not having the spiral ribs united at the poles.

35. *Oe. intermedium* Wittr.

36. *Oe. irregulare* Wittr.

37. *Oe. irregulare* Wittr. var. *condensatum* (Hallas) Hirn

38. *Oe. Landsboroughi* (Hass.) Wittr.

*39. *Oe. longicolle* Nordst. var. *senegalense* Nordst.

40. *Oe. macrandrium* Wittr. var. *aemulans* Hirn

[*Oe. macrandrium* Wittr. f. *aemulans* Hirn]

Vegetative cell 10–16×22–90μ; oogonium 28–42×33–45(–50)μ; oospore 26–36×26–36μ; dwarf male stipe 9–12×20–25μ; antheridium 6–9×7–10μ. Otherwise as in type.

Herb. C.E.T. 56.

This variety is characterized by the narrow vegetative cells and globose oospore. It differs from the form *lundense* by its longer vegetative cells.

41. *Oe. macrandrium* Wittr. var. *Hohenackerii* (Wittr.) Tiffany

42. *Oe. macrandrium* Wittr. var. *propinquum* (Wittr.) Hirn

43. *Oe. mexicanum* Wittr.

44. *Oe. mitratum* Hirn

45. *Oe. multisporum* Wood
46. *Oe. nebraskense* Ohashi
47. **Oe. oblongum** Wittr. **var. sphaericum** (Hallas) comb. nov. (fig. 21).

[*Oe. sphaericum* Hallas; *Oe. oblongum* Wittr. f. *sphaericum* (Hallas) Hirn]

Oospore globose to globose-ovoid; oogonium not completely filled by the oospore; vegetative cell 5–11×20–86μ; oogonium 21–28×30–52μ; oospore 16–27×16–30μ; antheridium 8–9×6–7μ. Otherwise as in type.

Herb. C.E.T. 232.

Hirn (1906) relegated *Oe. sphaericum* Hallas to *Oe. oblongum* Wittr. forma *sphaericum* (Hallas). Because of the appearance in the Oklahoma collections of material which extends the original description, but which undoubtedly belongs to this form, it has been given varietal rank.

*48. *Oe. oboviforme* Wittr.

This form had a slightly smaller oogonium; oogonium 59–63×76–99μ.

49. **Oe. ouchitanum** sp. nov. (figs. 22 and 23).

Oe. monocium, oogoniis singulis vel 2 continuis, pyriformibus vel subpyriformibus, operculo apertis, circumscissione superiore; oosporiis globosis (raro subglobosis), partem inferiorem vel submedianem, inflatam oogoniorum complentibus, membrana laevi; antheridiis ?–3, sparis, cellulis vegetativis capitellatis; cellula fili basali forma, ut vulgo, elongata; cellula fili terminali obtusa; cell. veget. 5–13×33–50μ; oogon. 30–33×33–40μ; oospor. 26–30×23–30μ; cell. antherid. 8–9×10–13μ.

Monoecious, oogonium 1–2, pyriform to subpyriform, opening by a superior operculum; oospore globose (rarely subglobose), not filling the oogonium longitudinally, wall smooth; antheridium ?–3, scattered; vegetative cell capitellate; basal cell elongate; terminal cell obtuse; vegetative cell 5–13 ×33–50μ; oogonium 30–33×33–40μ; oospore 26–30×23–30μ; antheridium 8–9×10–13μ.

Herb. C.E.T. 305.

The combination of capitellate vegetative cells and pyriform oogonia is the distinguishing character of this species, in that it is the only species in which the two are combined. It is to be compared with *Oe. simplex* and *Oe. pyrulum*, both of which have cylindrical vegetative cells, and with *Oe. pyriforme* and *Oe. pithophorae* which have cylindrical vegetative cells as well as different dimensions.

50. *Oe. paludosum* (Hass.) Wittr. var. *parvisporum* Hirn
51. *Oe. paucocostatum* Transeau
52. *Oe. plagiostomum* Wittr. var. *gracilius* Wittr.
53. *Oe. princeps* (Hass.) Wittr.
54. *Oe. Pringsheimii* Cramer; Wittr. var. *abbreviatum* Hirn (fig. 9)

Dioecious; vegetative cell 10–16×15–39μ; oogonium 28–33×29–36μ; oospore 27–30×27–30μ; antheridium 1-4, division horizontal, 9–14×5–10μ.

These dimensions combine the variations of the Oklahoma material with those of the original descriptions. The antheridia, heretofore unknown, are described and figured.

55. *Oe. pungens* Hirn

The length of the vegetative cells was 66-128μ. This exceeds the length given in the original description by 34μ.

56. *Oe. pusillum* Kirchner

*57. *Oe. rigidium* Hirn

Vegetative cell 14–16×38–54μ; oogonium 40–43×35–48μ; oospore 32–35×32–35μ. The oogonia are longer than in the type.

58. *Oe. Rothii* (Le Clerc) Pringsheim

59. *Oe. rufescens* Wittr. var. *exiguum* (Elfv.) Tiffany

60. *Oe. rugulosum* Nordst. var. *minutum* (Hansgirg) Hirn

61. *Oe. Sancti Thomae* Wittr. and Cleve

62. *Oe. suecicum* Wittr. var. *australe* (G.S.West) B.H.Smith

63. **Oe. subglobosum** sp. nov. (figs. 16–19).

Oe. dioicum, nannandrium, (?) idioandrosporum; oogoniis 2–10 continuis (raro singulis), globosis vel subglobosis, operculo apertis, circumscissione superiore; oosporiis subglobosis, oogonia fere complentibus, membrana laevi; cellulis vegetativis capitellatis; cellulis suffultoriis non vel paullulum tumidis; cellula fili basali forma, ut vulgo, elongata; nannandribus paullum curvatis, in oogoniis sedentibus, antheridio exteriore, uni-vel bicellulari; cell. veget. 13–20×49–83μ; cell. suffult. 23–33×39–43μ; oogon. 43–50×40–50μ; oospor. 40–46×36–40μ; stip. nannandr. 10–13×23–33μ; cell. antherid. 6–10×4–7μ.

Dioecious, nannandrous, (?) idioandrosporous; oogonium 1–10 (rarely single), globose to subglobose, superior operculum; oospore subglobose, quite filling the oogonium, spore wall smooth; vegetative cells capitellate; suffultory cell sometimes enlarged; basal cell elongate; dwarf male slightly curved, on the oogonium; antheridium 1–2, exterior. Vegetative cell 13–20×49–83μ; suffultory cell 23–33×39–43μ; oogonium 43–50×40–50μ; oospore 40–46×36–40μ; dwarf male stipe 10–13×23–33μ; antheridium 6–10×4–7μ.

Herb. C.E.T. 309.

This species together with *Oe. rigidium* are the only nannandrous species having the combination of superior position of the oogonial operculum, and capitellate vegetative cells. It is distinguished from the latter by the series of oogonia (1-10), subglobose oospore, and the larger size.

64. *Oe. tapeinosporum* Wittr.

The following is a summary of the new species and varieties named:

Bulbochaete alpina, B. areolata, B. cimarronea, B. Furberae Collins var. *depressa, Oedogonium concatenatum* (Hass.) Wittr. var. *regulare, Oe. flavescens* (Hass.) Wittr. var. *minus, Oe. illinoisense* Transeau var. *olkahomense, Oe. oblongum* Wittr. var. *sphaericum* (Hallas), *Oe. ouchitanum, Oe. subglobosum, Oe. fuscum.*

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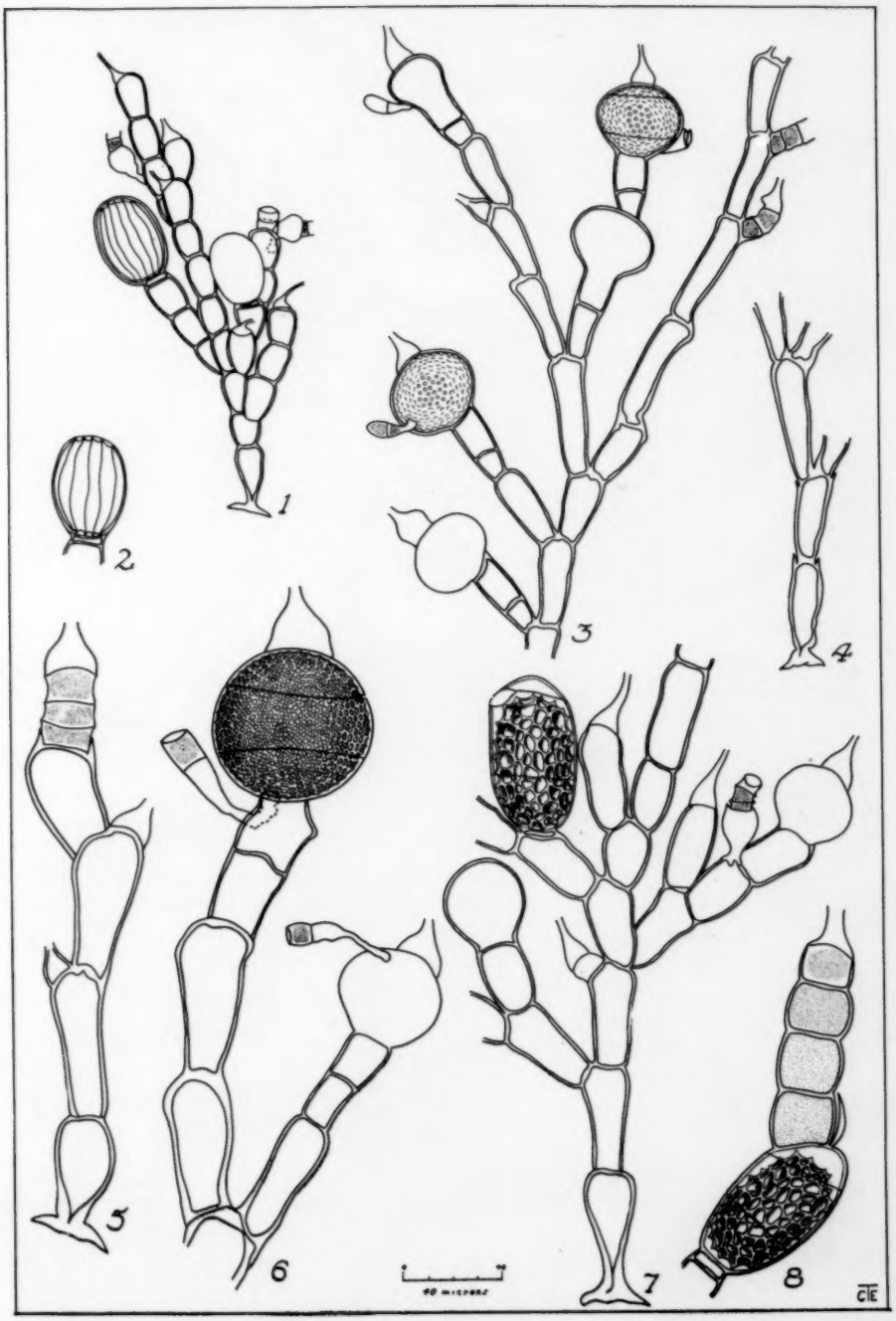
Explanation of plate 15

Figs. 1 and 2. *Bulbochaete cimarronea* Taft
Figs. 3 and 4. *B. Furberae* Collins var. *depressa* Taft
Figs. 5 and 6. *B. alpina* Taft
Figs. 7 and 8. *B. areolata* Taft

Explanation of plate 16

Fig. 9. *Oedogonium Pringsheimii* Cramer; Wittr. var. *abbreviatum* Hirn
Figs. 10–12. *Oe. flavescens* (Hass.) Wittr. var. *minus* Taft
Figs. 13–15. *Oe. fuscum* Taft
Figs. 16–19. *Oe. subglobosum* Taft
Fig. 20. *Oe. concatenatum* (Hass.) Wittr. var. *regulare* Taft
Fig. 21. *Oe. oblongum* Wittr. var. *sphaericum* (Hallas) Taft
Figs. 22 and 23. *Oe. ouchitanum* Taft
Figs. 24–26. *Oe. illinoisense* Transeau var. *oklahomense* Taft



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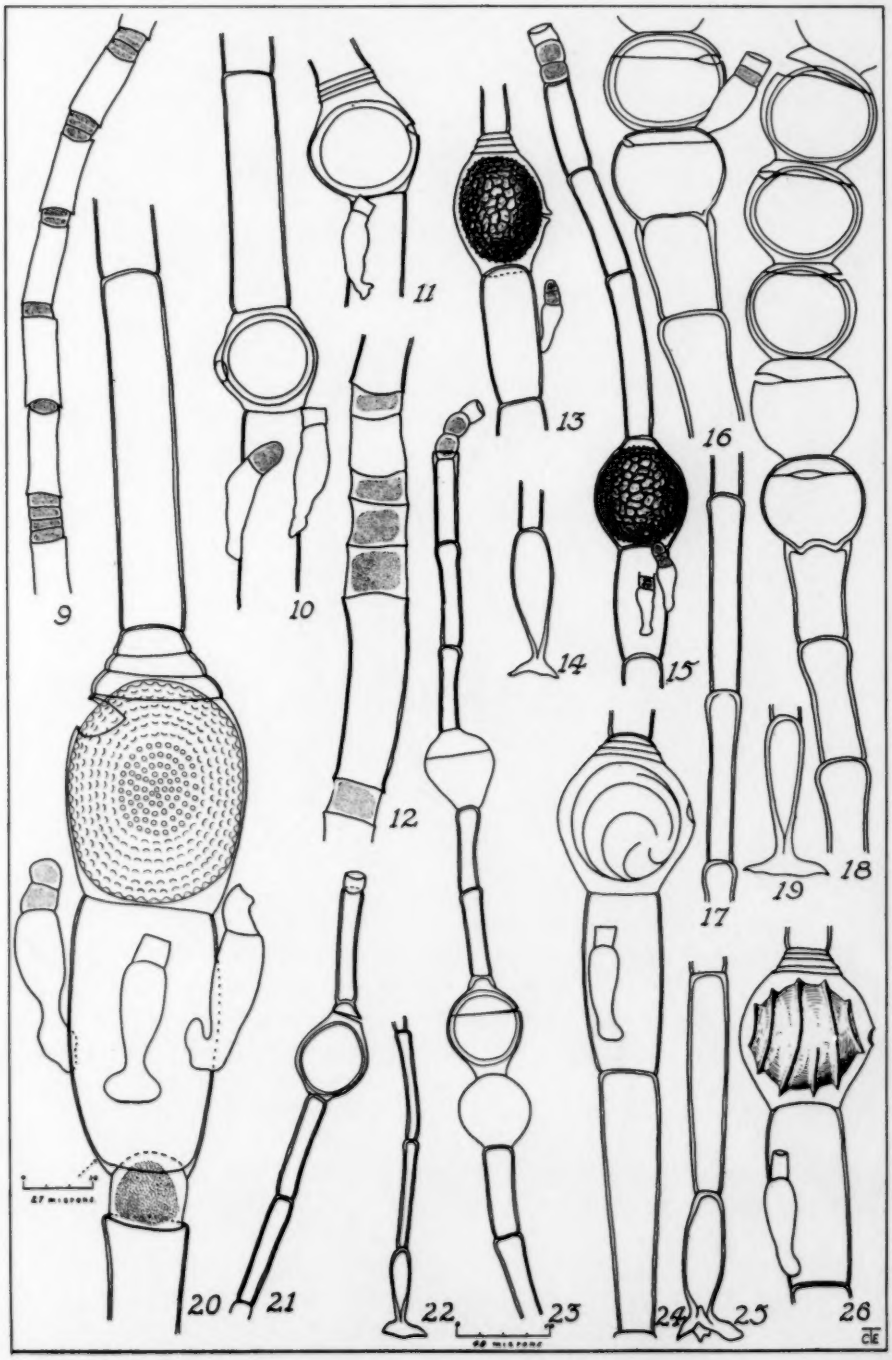

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INDEX TO AMERICAN BOTANICAL LITERATURE

1931–1935

The aim of this index is to Include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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